Riverscape-mediated effects of introduced trout on non-diadromous galaxiid fishes in New Zealand

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To my grandfather

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Contents

Abstract

The impact of invasive predators on native prey may depend on the availability and distribution of invader-free refugia across landscapes, if predators create demographic 'sink' populations in invaded patches, giving rise to source-sink dynamics in prey populations. Propagule pressure of immigrants dispersing from refugia (or sources) may consequently drive persistence in sink habitat, affecting predator-prey co-existence across the landscape. I studied whether introduced brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) create source-sink structuring in two native galaxiid fish species (*Galaxias vulgaris* and *G. paucispondylus*) in the rivers of the central South Island, New Zealand, and whether such dynamics affected the distributions of either species across river networks or "riverscapes". Young-of-the-year (YOY) *G. vulgaris* recruitment was rare in trout-invaded streams and consistently high in trout-free streams. Thus, trout-free reaches appeared to act as sources in a river network, while the majority of the trout-invaded riverscape was a demographic sink (i.e., no local recruitment occurred). Surveys of YOY *G. paucispondylus* did not reveal trout-induced source-sink dynamics, although mesocosm predation experiments suggested both species were highly vulnerable to predation by large trout. *Galaxias paucispondylus* recruitment was highest in intermittently flowing streams that were marginal habitats for trout, suggesting indirect interactions between trout and habitat affect *G. paucispondylus* distribution. Network configuration of trout-free source populations affected the distribution of *G. vulgaris,* as galaxiids were excluded from small streams with high bed stability that were far from sources. The interaction between propagule pressure and habitat gradients in mediating effects of trout on *G. vulgaris* distributions indicates habitat characteristics affect predator-prey interactions in a spatially explicit manner. Furthermore, the outcome of predator-prey interactions should be able to be modelled using habitat data alone if habitat consistently mediates predator impacts. I developed a GIS-based spatial model to predict where trout would exclude *G. vulgaris* in river networks, based on stream size and distance to galaxiid source populations. The model was tested in three different riverscapes using fish occurrence patterns obtained from electrofishing surveys, and successfully predicted *G. vulgaris* exclusion by trout. This further demonstrates the importance of habitat configuration in driving interspecific

interactions at the landscape scale. These findings suggest removing trout from small, stable tributaries to create new demographic sources could improve overall persistence of *G. vulgaris* across trout-invaded riverscapes. The galaxiid exclusion model should also be used to detect undiscovered trout-free source populations, and to aid in selecting streams for restoration of galaxiid populations through trout eradication.

Frontispiece: Hogs Back Creek, a trout-invaded tributary of the Broken River, Waimakariri Basin. A trout-free refuge stream for non-diadromous galaxiids enters the river via the small gorge at the head of the valley.

Chapter 1

General Introduction

Biological invasions pose a significant threat to biodiversity (Vitousek et al. 1996, Ricciardi 2007). Invasive predators in particular have had devastating effects on individual species and in some cases entire communities (Witte et al. 1992, Donlan and Wilcox 2008). This is especially true for freshwaters, where introduced predators have had a disproportionately large effect on local diversity (Cox and Lima 2006). A common culprit has been the human-mediated spread of predatory sports fish (Cambray 2003). Introductions and subsequent invasions of these fish have resulted in local extinctions, community shifts, trophic cascades and alterations to ecosystem functioning (Hall and Mills 2000, Donald et al. 2001, Simon and Townsend 2003, Finlay and Vredenburg 2007). To combat the spread of invasion, and to properly conserve the native communities affected, an understanding of the mechanisms involved is crucial (Hulme 2006). In the case of invasive fish species, the variability and patchiness of the receiving environment is likely a critical factor affecting invader success and their subsequent impacts (Moyle and Light 1996a, Gido and Brown 1999).

Habitat heterogeneity across ecosystems

In both aquatic and terrestrial systems, habitat patchiness affects establishment of invaders by limiting their distribution within fragments of suitable habitat (Byers 2002, Lee et al. 2009). Natural disturbance of the habitat can also positively or negatively mediate invasion success or impact, depending on the adaptations of native and non-native species to the disturbance (Meffe 1984, Fausch et al. 2001, Didham et al. 2005, McKenzie et al. 2007). A key potential outcome of habitat heterogeneity is the development of source-sink dynamics in populations. Marginal habitat that does not carry sufficient resources for survival or successful reproduction may have negative population growth and be prone to extinction (Pulliam and Danielson 1991, Thomas and Kunin 1999). These “sink” sites can be maintained by being rescued through immigration from “sources”, which have positive population growth and are net exporters of individuals over time (Pulliam and Danielson 1991, Dias 1996).

Source-sink dynamics can be involved in the establishment of non-native species in a novel environment, where populations at the invasion front are reinforced by propagule pressure from nearby invaded habitats (Meats et al. 2008). However, as an invasive predator establishes in the environment, it could have the potential to create source-sink dynamics within native prey species.

Predator-driven source-sink dynamics

Predation can create demographic sinks in invertebrate (Amezcua and Holyoak 2000, Caudill 2005) and vertebrate populations (Basse and McLennan 2003). If predator-occupied habitat is a sink, then factors such as local mortality and immigration can interact to determine the persistence of the prey species at a given locality in the invaded landscape (Pulliam and Danielson 1991). In the case of a predator-driven sink, predation pressure will likely drive mortality. Encounter rates between predators and prey can be mediated by relative species densities, hunting and avoidance behaviour, as well as habitat complexity and patchiness (Eklöv 1997, Binckley and Resetarits 2003, Ylönen et al. 2003, Hampton 2004, Kauffman et al. 2007). Immigration of prey into the habitat is a second potential driver of prey persistence in a predator-occupied habitat. Immigration rates would likely depend on the dispersal ability of the prey species (Baguette and Van Dyck 2007), and the locality of sources of immigrants (Nol et al. 2005). The configuration of sources and sinks in the landscape could therefore be critical in determining persistence of prey in a predator-dominated habitat.

Habitat configuration in rivers: the riverscape paradigm

Rivers possess a unique habitat structure where organisms are confined to linear pathways in dendritic networks (Fagan 2002). The shift in conditions from small headwater tributaries to large downstream rivers can affect community composition and ecosystem processes (Vannote et al. 1980, Thorp et al. 2006). In the case of mobile organisms like fish, the configuration and location of habitat can be critical drivers of individual species distributions (Schlosser 1991, Torgersen et al. 2006). Stream habitat is hierarchical and driven by multiple processes at different scales (Frissell et al. 1986). Freshwater fish populations are consequently driven by a complex interaction between landscape and reach-scale habitat variability (Schlosser and Angermeier 1995, Fausch et al. 2002). If interactions between mobile fish species and their environment are to be properly understood, it is crucial that they be investigated at multiple scales, and that the

spatial configuration of different habitats across the "riverscape" be considered (Labbe and Fausch 2000, Fausch et al. 2002, Le Pichon et al. 2006).

Where invasive predatory fish are present, their distribution in the landscape can have a direct impact on the distribution of native prey species (MacRae and Jackson 2001, Woodford et al. 2005). The effect of habitat heterogeneity and connectivity at different scales will itself lead to patchy distributions in the invader (Labbe and Fausch 2000, Spens et al. 2007). If predation pressure by the invasive fish is high enough to eliminate local recruitment of native species within occupied patches, then source-sink dynamics may arise in those species that disperse across the riverscape or landscape (Caudill 2005).

Model system: introduced trout and non-diadromous galaxiids in New Zealand

In this study I investigated the possible presence and implications of source-sink dynamics in native New Zealand fishes, driven by introduced trout. New Zealand contains a depauperate but highly endemic fish fauna, which includes at least 17 species of non-diadromous galaxiid (Salmoniformes: Galaxiidae) fishes, although more are in the process of being described (McDowall 2006). Trout have been viewed as a potential threat to non-diadromous galaxiid populations by concerned individuals since the early twentieth century (McIntosh et al. 2010), but only in the last 20 years has quantitative evidence of the impact of trout begun to emerge (Townsend and Crowl 1991, McIntosh 2000, McDowall 2006, McIntosh et al. 2010). Several local-scale mechanisms have been put forward to explain negative interactions (McDowall 2003a), but the landscape-scale effects of trout and the role of the landscape configuration of trout-free refugia have not been studied.

I investigated the influence of landscape-scale distributions of trout and habitat variability in affecting the distribution and structure of non-migratory galaxiid populations. I studied two species, the Canterbury galaxias (*Galaxias vulgaris* Stokell) and the alpine galaxias (*Galaxias paucispondylus* Stokell). Both sporadically co-occur with trout and are found in a variety of stream habitats (McIntosh 2000, Elkington and Charteris 2005), and so serve as excellent test species to understand the roles of habitat configuration and trout in driving the distributions and dynamics of threatened galaxiid populations.

Galaxias vulgaris (Figure 1) was once considered to be a phenotypically variable species that was widely distributed across the South Island (Townsend and Crowl 1991, Waters and Wallis 2001). Recent taxonomic revisions now recognise this "*G. vulgaris sensu lato*" species complex as a group of distinct species and as-yet undescribed taxa, which are collectively referred to as "flathead" and "roundhead" galaxiids (Waters and Wallis 2001, McDowall 2006, Burridge et al. 2007, Crow et al. 2009). Little is known about specific differences in ecology between these taxa, but it is possible that mechanisms found to drive trout impacts on *G. vulgaris* could be active in the interactions between trout and other species from this group. Similarly, *G. paucispondylus* (Figure 2) belongs to another group of morphologically distinct non-diadromous galaxiids, the "pencil galaxiids". These species are small, elongated and appear to prefer cold, fast-flowing rivers in spring-fed or high altitude streams (McDowall 2006), and are likely to share similar vulnerabilities to trout.

Thesis organisation

I have written my thesis as a series of stand-alone scientific papers intended for publication. There is therefore some overlap in the introduction and methods sections of the chapters. While many chapters are multi-authored, the writing and analyses are primarily my own, with contributions of co-authors listed in individual chapter acknowledgements. Figures and tables are numbered from the start of each chapter. Chapter Two has been accepted for publication in *Ecological Applications* and is currently in press.

In Chapter Two, I studied the population structuring of *G. vulgaris* inhabiting trout-invaded riverscapes, to assess whether trout create demographic sinks in these populations. I ascertained the relative importance of trout and habitat in driving *G. vulgaris* recruitment failure by combining a spatially continuous survey of juvenile recruitment across trout-invaded and trout-free reaches with quantitative monitoring of population structure at selected sites. The population structure of *G. vulgaris* at monitoring sites, combined with the spatially explicit census of sources and sinks, enabled the landscape-scale impact of trout on metapopulation stability to be interpreted.

Figure 1: The Canterbury galaxias, *Galaxias vulgaris* Stokell (Photo: Angus McIntosh)

Figure 2: The alpine galaxias, *Galaxias paucispondylus* Stokell (photo: Angus McIntosh)

Next, I assessed whether the demographic effects of trout on *G. vulgaris* identified in Chapter Two were likely to affect *G. paucispondylus,* and whether trout distributions or habitat could best explain the *G. paucispondylus* distributions in trout-invaded riverscapes. To establish the relative vulnerability of *G. vulgaris* and *G. paucispondylus*, I conducted predation experiments using mesocosms and fish manipulations in a natural stream in Chapter Three. The possibility of interactions between trout predation and abiotic habitat drivers of *G. paucispondylus* occurrence was assessed to explain riverscape-scale occurrence patterns.

In Chapter Four, I examined whether the spatial configuration of demographic sources identified in Chapter Two could be used to explain the landscape-scale occurrence patterns of *G. vulgaris*. The change in *G. vulgaris* biomass at sink sites with increasing distance to the nearest trout barrier was assessed to provide evidence of decreasing propagule pressure of immigrating fish as the distance between sources and sinks increases. The interaction between propagule pressure and local habitat variability in enabling *G. vulgaris* occurrence in trout-invaded reaches was then assessed by searching for limits in the distance the species could occur from trout-free source populations in the riverscape.

I used the spatial association between *G. vulgaris* occurrences in trout-invaded reaches and trout-free source populations described in Chapter Four to develop a GIS-based spatial model in Chapter Five that predicts exclusion of *G. vulgaris* by trout in invaded river networks. Transferability of the model across trout-invaded catchments was assessed, and applications in the conservation of *G. vulgaris* and other threatened fish were investigated.

Finally in Chapter Six, I review the implications of my research for the conservation of non-diadromous galaxiids in New Zealand, highlighting findings of importance to conservation managers and producing an integrated summary of the ecological drivers that affect *G. vulgaris* population persistence in trout-invaded riverscapes. I then expand on the conservation applications of the galaxiid exclusion model developed in Chapter Five and provide an example of its practical use in planning trout-removal programmes. I conclude the chapter by assessing the general lessons learned regarding native fish conservation in predator-invaded riverscapes.

Plate 1: Vulnerable *Galaxias vulgaris* fry swim in a backwater (Photo: Angus McIntosh).

Chapter 2

Evidence of source-sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout

ABSTRACT

Introduced predators with patchy distributions can create demographic sinks within native prey populations. Such invasions may give rise to source-sink metapopulations if there are still sources of native species colonists in the landscape. In New Zealand introduced brown (*Salmo trutta*) and rainbow trout (*Oncorhychus mykiss*) are linked with declines in native non-diadromous galaxiids, but co-occur with these galaxiids in some locations. I investigated whether trout create sinks in *Galaxias vulgaris* populations, and whether trout-free reaches could act as sources, allowing persistence in the sink habitat. I conducted quantitative seasonal monitoring of *G. vulgaris* population structure across two sub-catchments of the Waimakariri River, South Island. Two trout-free and seven trout-invaded sites in the Porter River catchment, as well as two trout-free and five trout-invaded sites in the Broken River catchment were monitored over two winters and the adjoining summer. Spatially continuous monitoring of young-of-the-year (YOY) galaxiid distributions and apparent survival across the Broken River catchment was also undertaken. *Galaxias vulgaris* YOY recruitment was high in trout-free reaches, indicating positive population growth. *Galaxias vulgaris* was absent from three trout-invaded sites, and the remaining invaded sites had significantly depleted juvenile recruitment. Information-theoretic model selection indicated trout rather than habitat drove recruitment failure. Trout-invaded sites could be divided into 'sinks' that retained no YOY galaxiids, indicating no local recruitment, and 'pseudosinks', which had very few recruits. Absence of small *G. vulgaris* at 'sink' sites suggested population maintenance through immigration of adults from sources, whereas 'pseudosink' sites appear capable of self-recruitment at low carrying capacities. Trout-free reaches appear to act as sources in a river network, but are susceptible to future invasions by trout. Thus, not only may invasive species cause source-sink metapopulations in native species, but the potential of refugia for natives (sources) to become future sinks highlights the vulnerability of these metapopulations when invasive predators are the principal demographic driver.

INTRODUCTION

Effective conservation of species depends on adequately understanding the environmental and biotic pressures that structure populations (Shaffer 1981, Lande 1988). Variation in habitat suitability means populations tend to be patchily distributed within landscapes (Turner 1989), and many species form source-sink metapopulations, where extirpation from low productivity sink patches is prevented by immigration from high-productivity source patches (Pulliam and Danielson 1991, Dias 1996). While source-sink dynamics may be driven by differences in food availability or habitat for critical life-history stages among patches (Foppen et al. 2000, Nol et al. 2005, Sulkava et al. 2007), they can also be driven by predators (Amezcua and Holyoak 2000, Caudill 2005).

Invasions by non-native predators may give rise to source-sink systems in native prey populations. Invasion is often patchy, negatively affecting vulnerable native prey species to varying degrees through the landscape (Maret et al. 2006). Consequently, invader-free patches may act as sources for adjacent predator-invaded sinks (Basse and McLennan 2003). To assess whether source-sink dynamics can facilitate predator-prey co-existence, I examined the population structuring of a vulnerable native fish species within river networks containing an introduced predator.

The patchy distribution of critical habitat and fish across the landscape of a river network, or 'riverscape' (*sensu* Fausch et al. 2002), means that fragmented metapopulations can form within those networks (Rieman and Dunham 2000, Koizumi and Maekawa 2004, Slack et al. 2004). The patchy distribution of introduced predatory fish may also be an important driver of such metapopulations, as they can fragment populations of vulnerable fish species (Labbe and Fausch 2000). Introduced fish have had severe impacts on native freshwater fish species around the world, sometimes resulting in local extinctions (Witte et al. 1992, Lintermans 2000, Woodford et al. 2005), and generally increasing overall extinction risks by fragmenting populations (Labbe and Fausch 2000, Fagan 2002). If sufficient individuals are able to disperse from refugia into predator-occupied habitat, populations that would normally go extinct may be rescued (Amezcua and Holyoak 2000). Source-sink dynamics may therefore explain native fish

co-existence with an introduced predator, if the river system still contains predator-free refugia.

The Canterbury galaxias (*Galaxias vulgaris* Stokell) (Salmoniformes: Galaxiidae), a benthic, stream-dwelling fish (McDowall 2000), is one of 15 non-diadromous galaxiids endemic to the rivers of New Zealand, and part of a species flock including several newly described taxa and genetically distinct lineages (Waters et al. 2000, McDowall 2006). All these galaxiid taxa are potentially threatened by predatory brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum), introduced for angling over a century ago (McDowall 2006). For example, three species within the galaxiid species group, *G. anomalus*, *G. pullus*, and *G. eldoni*, have restricted ranges in the Taieri River catchment, where they only survive above waterfall barriers that prevent further invasion by *S. trutta* (Townsend 1996). *Galaxias vulgaris*, in contrast, inhabits many trout-invaded streams, often in sympatry with trout (Cadwallader 1975, Glova et al. 1992, McIntosh 2000, Davey and Kelly 2007). Avoidance behaviour, microhabitat segregation and reductions of large trout through flooding have all been proposed to explain their co-existence (McIntosh et al. 1992, Edge et al. 1993, Glova and Sagar 1993, McIntosh 2000).

I tested the hypothesis that source-sink metapopulation dynamics enable the persistence of *G. vulgaris* in invaded riverscapes, with trout-invaded reaches acting as sinks but *G. vulgaris*-occupied reaches above barriers to trout invasion acting as sources. There is a paucity of studies empirically demonstrating source-sink dynamics in nature, since this generally requires estimates of both patch-specific population growth rates and individual dispersal rates (Diffendorfer 1998), and measuring these in freshwater fish is especially difficult (Dunham and Rieman 1999, Koizumi and Maekawa 2004). Instead I used fish distributions and survivorship to infer population structuring mechanisms, since it is possible to infer source-sink dynamics by monitoring the success of critical life-history stages (Caudill 2003, Caudill 2005). In addition, I considered the alternative possibility that apparent source-sink patterns were driven by physical habitat conditions.

METHODS

Study area

The study was undertaken in two sub-catchments of the upper Waimakariri River, which drains the eastern slopes of the Southern Alps, South Island, New Zealand (Figure 1). The sub-catchments included four tributaries of upper Broken River and three tributaries of upper Porter River, habitat-diverse riverscapes where both trout and galaxiids occur (McIntosh 2000, Jellyman and McIntosh 2008). A principal source of diversity of stream habitat in the system is flood-driven disturbance, which can be high and unpredictable in mountain-runoff streams, or low and predictable in spring-fed streams where the majority of instream flow is groundwater-derived (Jowett and Duncan 1990). Sixteen quantitative fish monitoring sites were established on the mainstems and selected tributaries within these sub-catchments (Figure 1). These sites covered the full range of habitat variability and included four sites above and twelve sites below barriers to trout invasion (natural waterfalls, road culverts and seasonally drying reaches that limited trout movement).

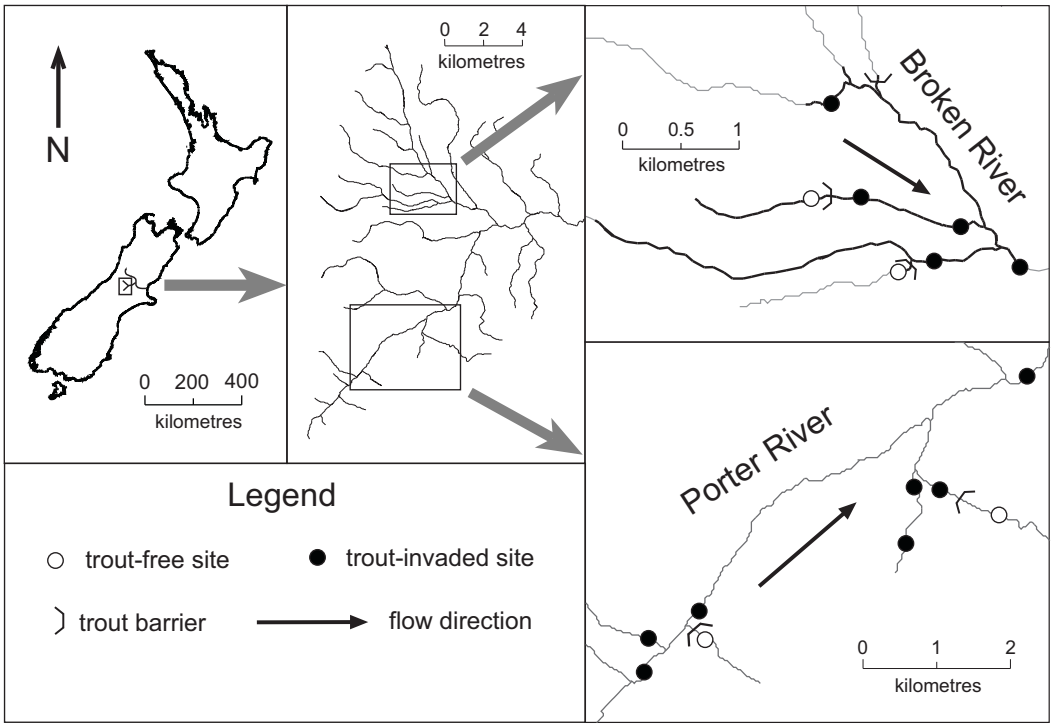

Figure 1: Map of study area, showing the location and extent of the surveyed Porter and Broken riverscapes and the position of quantitative monitoring sites within each riverscape. The reaches of Broken River monitored during fry surveys are drawn in bold.

Continuous riverscape analysis of fry distribution and apparent survival

To investigate how *G. vulgaris* demography differs across a partially trout-invaded riverscape, I surveyed the distribution, density and apparent survival of post-larval *G. vulgaris* across the Broken River network. Logistical and weather-related complications meant a survey on the Porter River could not be completed. *Galaxias vulgaris* larvae are positively rheotactic immediately after hatching (Cadwallader 1976a), and disperse in the water column until swept into backwaters, where they remain until large enough to actively swim in the main channel (Jellyman and McIntosh 2008). The fry (post-larval fish trapped in backwaters, *sensu* Jellyman and McIntosh 2008) are slow-swimming and constantly pelagic within the still and shallow backwaters, making visual density estimates possible. The fry appear in the austral spring (November), and leave the backwaters in autumn especially from March to April (Jellyman and McIntosh 2008).

Fry were surveyed in summer (December 2007) and autumn (March 2008). This allowed the assessment of fry distributions at peak abundance and at the end of the summer, when they were close to leaving the backwaters. Because backwater fry densities decline in the latter part of the season, due to a likely combination of biotic, abiotic and density-dependent drivers of mortality (P. G. Jellyman, University of Canterbury, unpublished data) as well as possible early emigration, the numbers remaining in autumn could be interpreted as apparent survival of the fry cohort (*sensu* Coleman and Fausch 2007). Fieldwork consisted of one or two researchers walking upstream, estimating available backwater area and counting *G. vulgaris* fry. Backwater area was visualised as squares of surface area that best covered the backwater. Visual estimates were highly correlated with measured backwater area ($n = 38$, $r = 0.96$, $p < 0.001$) with a fitted regression slope of 1. Rectangular measurements of backwater area provided a logistically feasible field measure, which I assumed had a small, consistent margin of error across the riverscape. To validate visual counts in summer, fry numbers were estimated in a sub-set of backwaters and then removed by hand with a dip net and re-counted in white trays. Due to the lack of cover-seeking behaviour in summer fry, complete removal by dip netting was possible. Numbers counted in removal sampling were highly correlated with those from visual estimates ($n = 13$, $r = 0.93$, $p < 0.001$). The slope of the relationship between netting and visual counts was 0.71, indicating slight underestimation of fry numbers. Surveys therefore represented consistent minimum estimates of actual backwater densities. Fry counts could not be

similarly verified in autumn, due to the increased swimming ability of the fry making dip-net capture impractical. Since 89% of autumn fry counts were ≤5 fish per backwater, and fry remained pelagic within the backwaters, I assumed survey estimates involved a small margin of error that was consistent across the riverscape.

The river network was divided into contiguous reaches of 30-100 m, and reach ends were marked on a Trimble© Geo-XM portable GPS. Co-ordinates were differentially corrected to a horizontal accuracy of two to ten metres, and estimated fry numbers and backwater area summed for each reach. Stream width was measured at each reach end so that a continuous estimate of stream size could be used in assessing the effect of riverscape-scale habitat change on fry distributions. Dense forest fragments inhibited the GPS signal on two trout-free streams and prevented us monitoring fry across all trout-free reaches. I consequently only surveyed trout-free reaches downstream of the forests, and focussed my efforts assessing fry distributions across the trout-invaded riverscape. At the conclusion of the autumn survey, I searched the trout-free reaches upstream of the forest fragments for fry to better assess the relative proportion of potential source and sink habitat occurring across the fish-occupied riverscape. In total 12.7 km of stream was traversed.

Fry density estimates in summer and autumn were mapped using ArcGIS 9.1 (ESRI 2005). The length of stream where fry did or did not persist until the end of autumn, in trout-invaded or trout-free reaches was calculated using the cumulative lengths of digitised segments in the GIS. To examine whether trout distribution or stream width could best describe fry density, a range of candidate models were compared using the Akaike Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson 2002). Candidate models were fitted via least squares and included: (1) univariate models with trout (presence/absence) and width as predictors; (2) an additive model including trout and width; and (3) a model including trout, width and an interaction between trout and width, with fry density as the response. The AIC_c and AIC weights were computed for each model based on its residual sum of squares. The difference between each model's AIC_c and the best (lowest scoring) model's AIC_c, or Δ AIC_c, was calculated (Burnham and Anderson 2002). Models with $|\Delta\ AIC_c| < 2$ were regarded as similarly informative as the best model. If the best model/models included more than one parameter, the importance scores of each parameter were calculated from

the combined AIC weights of models including the parameter (Burnham and Anderson 2002). Fry densities were square-root transformed to meet the normality and homoscedasticity assumptions required for regression analysis.

Quantitative fish monitoring

Depletion electrofishing with a Kainga EFM 300 backpack electrofisher (NIWA instrument Systems, N.Z.) generating 400-600V pulsed DC current was conducted at all monitoring sites in late winter (September 2006) and summer (February 2007), to quantify the population structuring of *G. vulgaris*. A second winter survey (August 2007), at all sites where *G. vulgaris* had been recorded previously, was used to assess survival of recruits. At each site, 20 metres of stream were delineated by stop-nets and three depletion passes were conducted. The surveyed area was fished using sequential sweeps downstream into a metre-wide push net, ending at the downstream stop net. The stop net was checked for fish after every pass. This method is standard practice for collecting benthic galaxiids in New Zealand (McIntosh et al. 1994). All fish captured were weighed and measured (nearest 0.1 g and 1 mm, respectively) and returned to the stream. All native fish were measured to total length (TL) as they have square or rounded tails, while trout were measured to fork length (FL). The total abundance of each fish species were estimated from three-pass depletion data using the maximum weighted likelihood formula of Carle and Strub (1978) and divided by stream surface area to obtain density per unit area. Fish densities were multiplied by the mean biomass per species per site to obtain biomass data.

Galaxias vulgaris were grouped into three size classes: 0-60 mm, 61-90 mm, and >90 mm TL corresponding to young-of-the-year (YOY), one-year-old fish, and 2+ year-old fish, respectively. These categories were based on the relationship between length and the formation of otolith annuli (Cadwallader 1973), and the maximum length of YOY fish previously recorded in the Waimakariri catchment in September (Benzie 1968). Both male and female *G. vulgaris* are sexually mature after one year (Cadwallader 1976b), so 1 and 2+ fish are referred to as small and large adults, respectively. The absence of YOY fish is a good indicator of sink habitat (Driver et al. 2005), whereas a population with some recruits could theoretically maintain itself in the absence of immigration at low carrying capacity, making the habitat a 'pseudosink' (Dias 1996, Pulliam 1996). Consequently, trout-invaded sites that contained *G. vulgaris* were

divided post-hoc into sites with and without YOY recruits, distinguishing pseudosinks from sinks. Overall biomass of *G. vulgaris* at source, sink and pseudosink sites were compared using repeated measures ANOVA. Seasonal densities of YOY, small adults and large adults at source, sink and pseudosink sites were compared using repeated measures MANOVA, followed by one-way repeated measures ANOVA. I chose to compare size classes using density rather than biomass as this gave a less biased assessment of cohort success, which was heavily skewed by the weight difference among size classes. The seasonal biomass of trout at sink and pseudosink sites was also compared using repeated measures ANOVA.

Habitat analysis and model testing

After electrofishing in September 2006, discharge was measured on a transect using a Marsh-McBurney electromagnetic flow meter mounted on a top-setting wading rod, width and three depths were measured at downstream, middle, and upstream limits of the reaches, and 30 streambed particles were randomly selected from the site and their longest axis recorded. Percentage cover of submerged and emergent aquatic vegetation was visually estimated, as well as cover by overhanging riparian vegetation. The flow-related disturbance regime of the stream was assessed using the river disturbance index (Pfankuch 1975), a subjective index that uses upper, middle bank and riverbed characteristics to assign a numerical disturbance rating that correlates strongly to substrate movement caused by flooding (Death and Winterbourn 1994, Greenwood and McIntosh 2008). Water temperature and stage were monitored in each tributary with WT-HR stage-height loggers (Trutrak, Christchurch, NZ).

To compare habitat among monitoring sites, Principle Components Analysis (PCA) was performed on physical habitat variables, producing factors that summarised variation in habitat (PCA 1 and 2 hereafter). The potential status of trout-free sites as outliers in overall habitat variation was tested using Student t-tests between the factor co-ordinates of trout-free and all other sites. To assess whether habitat was a stronger predictor of source-sink dynamics at monitoring sites than trout, regression models describing biomass of YOY *G. vulgaris* in the two winter surveys were fitted and compared using Δ AIC_c. I only compared sites where *G. vulgaris* occurred. The summer survey was not used, as fry were still transitioning from backwaters to the river channel at the time of the survey, making electrofishing results potentially spurious. Candidate models

included: (1) univariate models with trout presence, PCA 1 or PCA 2; (2) additive models with trout and either PCA axis, and (3) and additive model with just the PCA axes. To avoid over-parameterisation given my small sample size, I limited models to a maximum of two predictors and did not consider interactions. All biomass data were square root transformed, continuous habitat data were $\log_e$-transformed, and all percentage data were arcsine-square root transformed to meet statistical assumptions. All statistical analyses were performed in Statistica 8 (Statsoft 2007).

RESULTS

Fry distribution and interactions with trout and habitat

In summer 2007, the season of peak galaxiid fry abundance (Jellyman and McIntosh 2008), *G. vulgaris* fry were found in high densities across most of the surveyed riverscape of the Broken River (Figure 2a). Backwaters were recorded in 86% of trout-free segments with a mean estimated area of 2.83m^2 per segment. Backwaters occurred in 96% of trout-invaded reaches (2.28 m^2 per segment). By autumn 2008, fry were no longer present in most trout-invaded reaches, but persisted in most trout-free reaches (Figure 2b). While estimated backwater area in trout free reaches decreased to 1.7 m^2 per reach (63% of reaches retained backwater) and 1.36m^2 in trout invaded reaches (89% retained backwater), there was no significant difference in backwater area per segment between trout- invaded and trout-free reaches in summer ($t = 1.4$, $df = 171$, $p = 0.16$) or autumn ($t = 1.21$, $df = 171$, $p = 0.23$). Apparent fry survival (estimated autumn density) was higher among trout free reaches than trout invaded reaches ($t = 7.48$, $df = 171$, $p < 0.0001$). Trout-free reaches retaining fry (including previously unmonitored reaches upstream of forest fragments) made up 16% of the surveyed river network, while trout-invaded reaches retaining fry made up 7% of the surveyed network (Table 1). Invaded segments that retained fry were scattered across the riverscape, often isolated from each other by more than a kilometre (Figure 2b).

AIC_c model selection indicated that a model containing trout, width and trout x width interactions best described overall fry density in summer (Table 2, model a). The interactive model had an AIC weight several orders of magnitude higher than either trout-only or stream width-only models. Given the overwhelming weight of this model, the importance of individual trout or stream width effects could not be assessed.

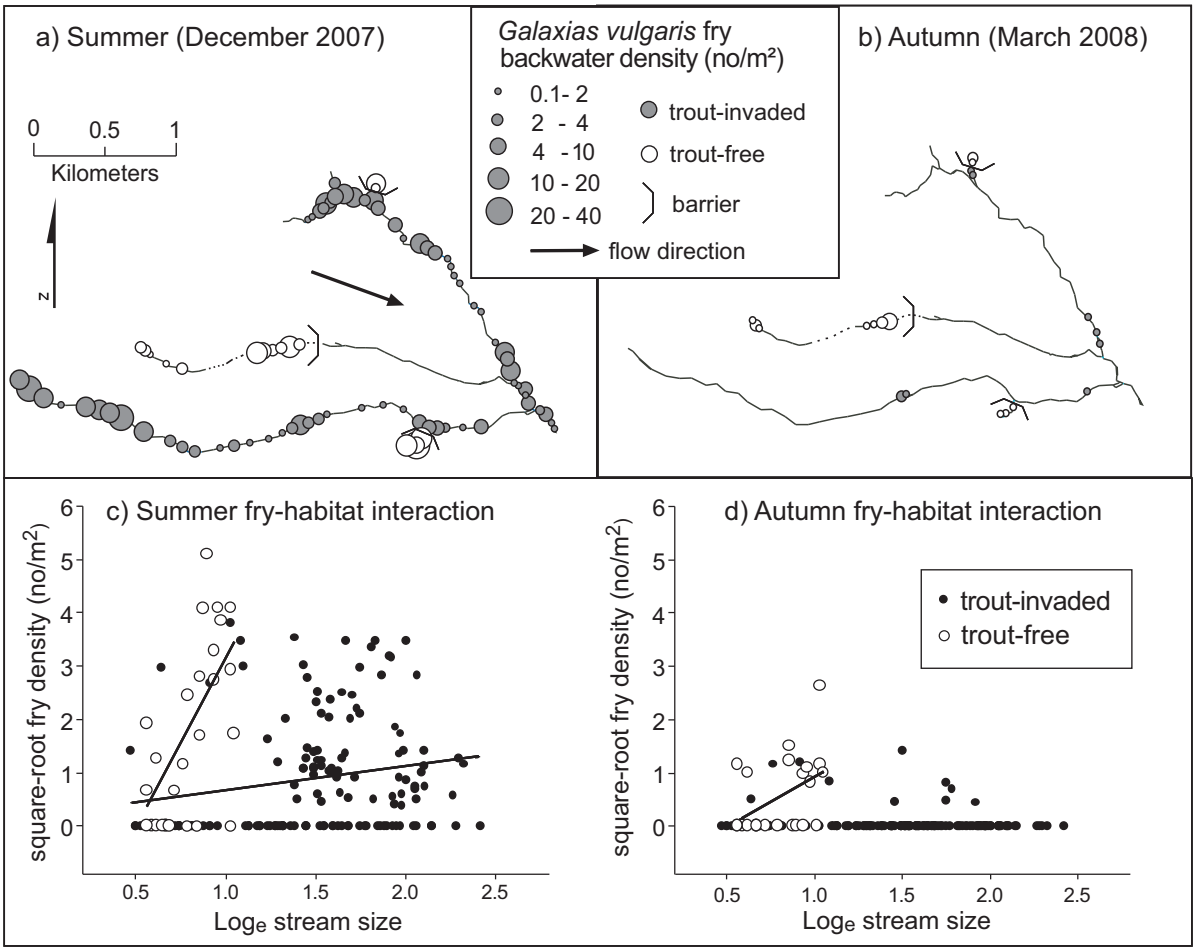

Figure 2: Maps of *G. vulgaris* fry density estimates and distributions recorded across the monitored Broken River network in a) summer (December 2007), b) autumn (March 2008), as well as the interaction between fry density and stream size within trout-free and trout-invaded reaches in c) summer, and d) autumn. Dashed lines in the stream network represent seasonally drying reaches. Lines on density graphs indicate significant ($p < 0.05$) relationships between fry density and stream size above and below trout barriers, fitted by least-squares regression.

Trout presence negatively affected the strength of the relationship between initial fry densities and stream width (Table 3, model a; Figure 2c). While there was no overall correlation between fry density and stream width ($r = 0.06$, $p = 0.43$), densities were positively associated with stream width when trout and trout-free reaches were examined separately (i.e. $r = 0.66$, $p < 0.001$ above trout barriers and $r = 0.21$, $p = 0.01$ below barriers; Figure 2c). In autumn, fry density was again best described by a model including additive and interactive trout and stream width effects (Table 2, model b), but the relationship of fry density to width differed from that observed in summer (Figure 2d). Autumn density above barriers was still positively associated ($r = 0.47$, $p = 0.01$) with stream width, whereas fry in the trout-invaded riverscape were randomly distributed across the stream width gradient (Figure 2d).

Table 1: Cumulative lengths of Broken River network segments where galaxiid fry were retained or not retained through to March in barrier or trout-invaded reaches. Surveyed reaches included trout-free reaches upstream of forest fragments not initially monitored in December but checked for the presence of fry in March. Segments monitored in December and March are shown in Figure 2.

	Trout-free reaches with no fry recruitment/ retention	Trout-free reaches retaining fry – "sources"	Trout-invaded reaches retaining no fry – "sinks"	Trout-invaded reaches retaining fry – "pseudosinks"
Cumulative surveyed segment length (m)	1069	2026	8773	877
Percentage of trout-free or trout-invaded network surveyed	29	65	91	9
Percentage of total river network surveyed	8	16	69	7

Table 2: Selection of linear models to describe fry backwater density and YOY biomass through Δ AIC_c analysis. All candidate models with an AIC weight ≥10% of the best model's weight are shown. For each analysis, top models were regarded as those with a Δ $AIC_c < 2$.

Analysis	Model	K	RSS	AIC	AIC_c	Δ AIC_c	AIC w
Fry density (summer 2007)	a) trout + width + (trout x width)	5	201.61	36.48	36.84	0.00	1.00
Fry density (autumn 2008)	b) trout + width + (trout x width)	5	14.63	-417.32	-416.96	0.00	1.00
YOY biomass (winter 2006)	c) trout	3	0.07	-55.53	-52.53	0.00	0.56
	d) trout + PCA2	4	0.05	-56.77	-51.06	1.47	0.27
	e) trout + PCA1	4	0.06	-55.29	-49.57	2.95	0.13
YOY biomass (winter 2007)	f) trout	3	0.11	-50.77	-47.77	0.00	0.72
	g) trout + PCA2	4	0.09	-50.02	-44.31	3.46	0.12
	h) trout + PCA1	4	0.10	-49.38	-43.66	4.10	0.09

Table 3: Parameter estimates for top models predicting *G. vulgaris* fry densities across the riverscape and YOY biomass across quantitative monitoring sites.

Analysis (Model)	Model Parameter	Estimate (95% confidence limits)
Fry density summer 2007 (a)	intercept	-1.75 (-2.84, -0.68)
	trout presence	1.88 (0.80, 2.96)
	width	3.59 (2.30, 4.89)
	trout x width	-3.10 (-4.39, -1.81)
Fry density autumn 2008 (b)	intercept	-0.51 (-0.79, -0.21)
	trout presence	0.54 (0.26, 0.83)
	width	0.99 (0.65, 1.34)
	trout x width	-0.99 (-1.34, -0.65)
YOY biomass winter 2006 (c)	intercept	0.11 (0.05, 0.17)
	trout presence	-0.11 (-0.17, -0.05)
YOY biomass winter 2006 (d)	intercept	0.09 (0.04, 0.16)
	trout presence	-0.12 (-0.17, -0.06)
	PCA2	0.03 (-0.01, 0.08)
YOY biomass winter 2007 (f)	intercept	0.13 (0.06, 0.20)
	trout presence	-0.08 (-0.15, -0.01)

Monitoring sites: Fish and habitat patterns

Galaxias vulgaris was recorded at all trout-free sites in all three sampling seasons. At least one species of trout (*O. mykiss*) was recorded at all sites below trout barriers, and both *O. mykiss* and *S. trutta* were recorded at two sites (Table 4). *Galaxias vulgaris* was never recorded at three trout-invaded sites, while one or more size classes of *G. vulgaris* were present at the other nine sites containing trout. Other fish species encountered at both trout-free and trout-invaded sites were the New Zealand longfin eel (*Anguilla dieffenbachii* Gray) and the alpine galaxias (*G. paucispondylus* Stokell). Only one species, the upland bully (*Gobiomorphus breviceps* Stokell), was recorded just at trout-invaded sites.

Table 4: Galaxiid-trout species co-occurrence scenarios at sites above and below trout barriers, indicating whether or not young-of-year *G. vulgaris* were ever recorded at any sites within the category in two years of sampling, and the number of sites in each category.

Location relative to trout barriers	Species present	*Galaxias vulgaris* YOY present	Number of sites
Above barrier	*G. vulgaris* only	Yes	4
Below barrier	*G. vulgaris* + *O. mykiss*	Yes	4
Below barrier	*G. vulgaris* + *O. mykiss*	No	3
Below barrier	*G. vulgaris* + *O. mykiss* + *S. trutta*	No	2
Below barrier	*O. mykiss* only	Not Applicable	3

The first two PCA factors explained most of the variability in habitat structure among quantitative monitoring sites (58.8% and 18.9%, respectively). PCA 1 was positively associated with width, depth, discharge and disturbance, and negatively associated with bank vegetative cover. PCA 2 was positively associated with disturbance and negatively associated with habitat depth, substrate particle size and aquatic vegetative cover (Figure 3b). Trout-free sites tended to be small and shallow with relatively high flow stability, but were not outliers in the overall spread of sites in ordination space (PCA 1: $t = 1.41$, $df = 14$, $p = 0.18$; PCA 2: $t = -0.33$, $df = 14$, $p = 0.74$) and overlapped with sites containing trout (Figure 3a).

AIC_c model selection indicated YOY biomass was best described by trout presence alone in winter 2007, while models with trout only and trout + PCA 2 were equally informative predictors of YOY biomass in 2006 (Table 2). Trout presence had a negative effect on YOY biomass in both analyses, and had a higher importance score than either habitat factor in the 2006 dataset (trout = 0.96, vs. PCA 1 = 0.14 and PCA 2 = 0.27); the trout effect was three times more important than habitat in the 2006 model. In terms of habitat variables captured in PCA 1 and 2, trout-invaded sites that retained recruits (i.e. pseudosink sites) were large, disturbed, or both (Figure 3).

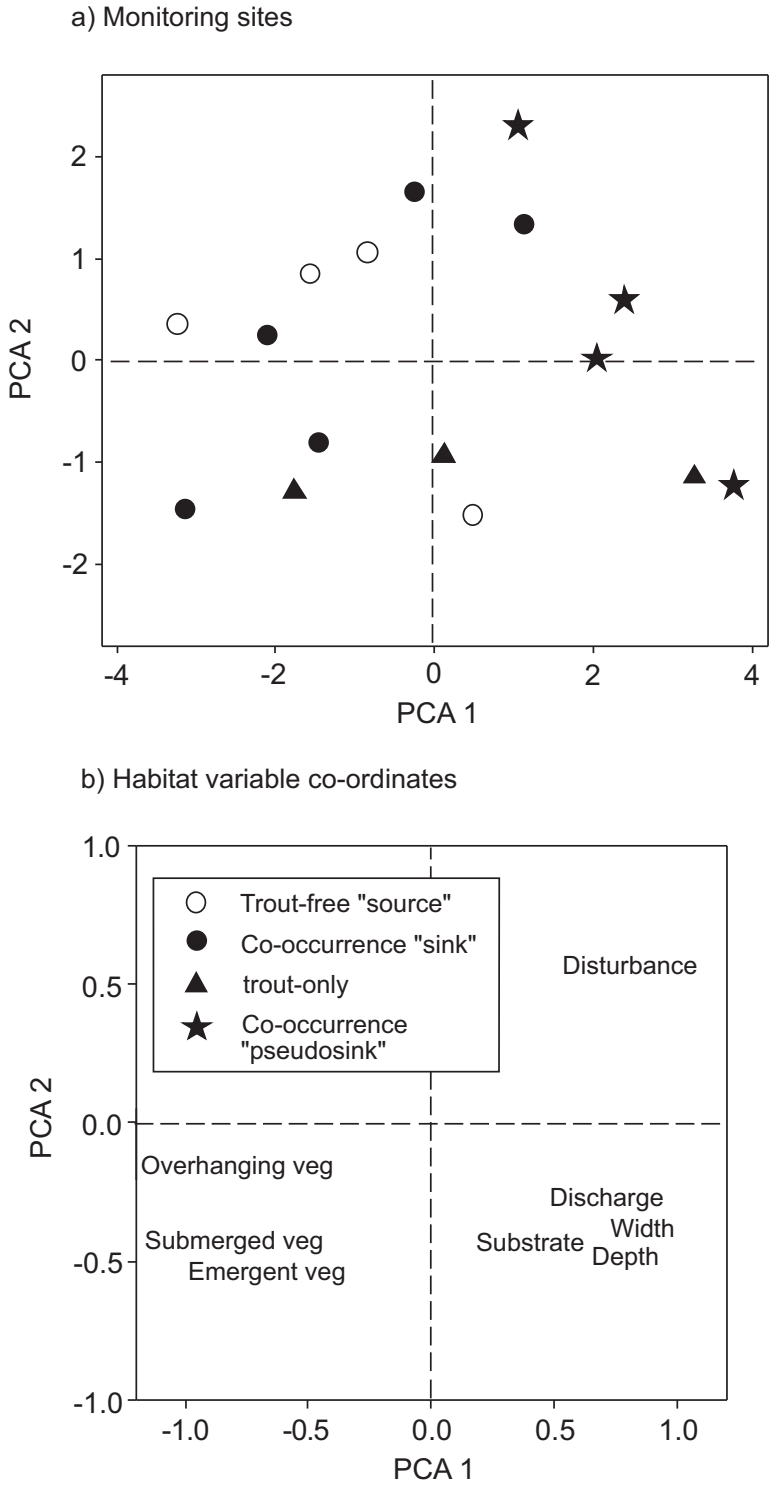

Figure 3: Principle components analysis of monitoring sites showing a) the co-ordinates of monitoring sites across the first two PCA factors, b) the co-ordinates of habitat variables across these factors. Co-ordinates indicate strength and directionality of each site or habitat variable's relation to PCA factors.

Biomass and size structuring of *Galaxias vulgaris*

Galaxias vulgaris biomass was significantly different among putative source, sink and pseudosink sites (Table 5). Post hoc Tukey HSD tests indicated *G. vulgaris* biomass at trout-free sites was higher than at pseudosink sites ($p < 0.02$). Trout biomass differed significantly between sinks and pseudosinks, as well as among seasons (Table 5). Post hoc Tukey HSD tests indicated trout summer biomass was higher in sinks than at pseudosinks in winter ($p < 0.02$).

Table 5: Repeated measures univariate and multivariate ANOVAs testing differences in seasonal biomass of trout and *G. vulgaris*, as well as seasonal densities of YOY, small and large adult *G. vulgaris* between putative sources, sinks and pseudosinks. Only significant effects are shown.

Effect	Wilks λ	df (num, den)	F	p
***G. vulgaris* biomass ANOVA**				
Source-sink		2, 8	6.06	0.02
Trout biomass ANOVA				
Sink-pseudosink		1, 5	10.55	0.02
Season		2, 5	4.73	0.03
***G. vulgaris* density MANOVA**				
Source-sink	0.13	6, 14	4.21	0.01
Source-sink x season	0.02	12, 8	4.53	0.02
YOY density				
Source-sink		2, 8	6.04	0.02
Source-sink x season		4, 8	3.29	0.03
Small adult density				
Source-sink		2, 8	7.02	0.01
Large adult density				
No significant effects				

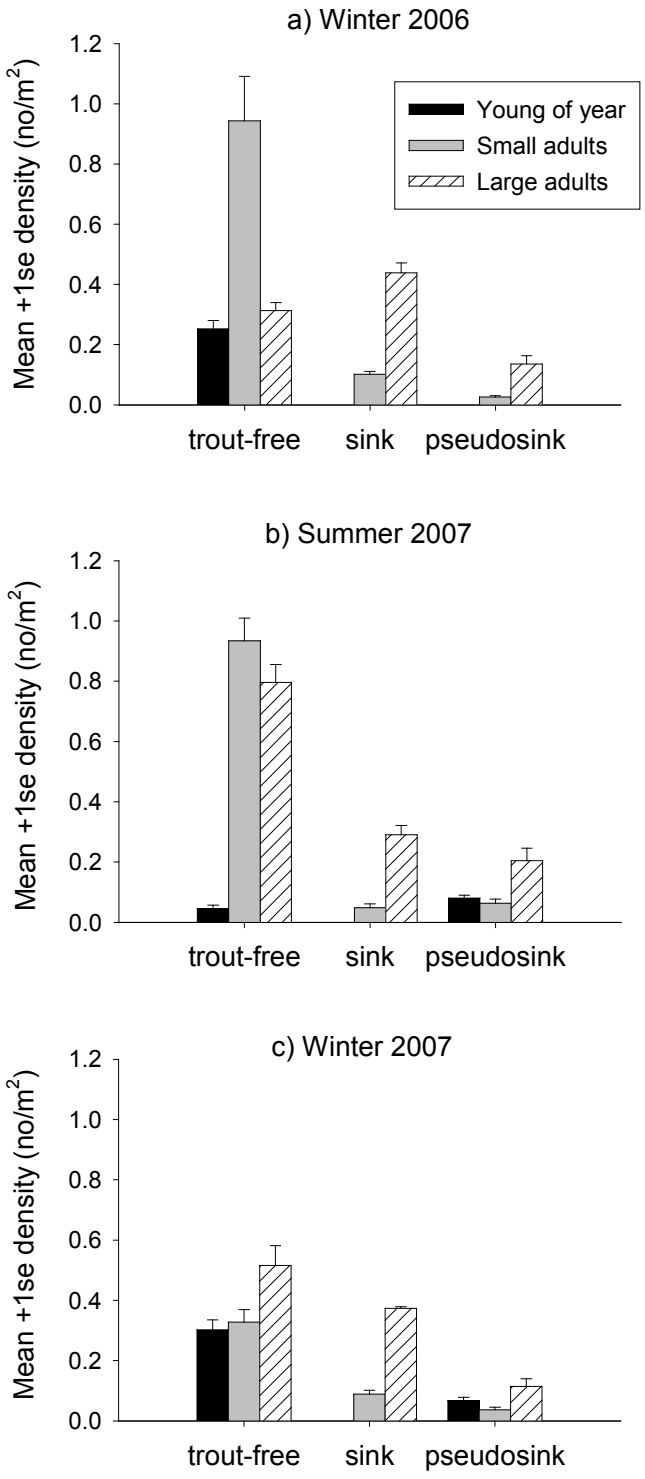

Figure 4: Mean (+1 SE) density of three size classes (YOY – 30-60 mm; small adult – 61-90 mm, large adult – >90 mm) of *G. vulgaris* recorded at trout-free sites, trout-invaded "sink" sites where *G. vulgaris* occurred, and all invaded "pseudosink" sites in a) winter 2006, b) summer 2007 and c) winter 2007.

While large trout (>150mm FL) were rarely captured in pseudosink sites, they were captured at all sink sites, as well as all sites where *G. vulgaris* was entirely absent. Densities of *G. vulgaris* size classes varied among the demographic categories of trout-free, sinks and pseudosinks, with a significant interaction with sampling season (Table 5). The interaction between demographic categories and season indicates differences in YOY and small adult *G. vulgaris* density among trout-free and trout-invaded sites fluctuated as the seasons changed. Post hoc Tukey HSD tests showed YOY density was significantly higher at trout-free sites than either sink or pseudosink sites ($p = 0.04$; Figure 4). Likewise small adults (61-90 mm) were found in significantly higher densities at trout-free sites than either sinks or pseudosinks (Table 5, Figure 4). Large adult (>90 mm) densities were not significantly different across the three demographic categories (Table 5), although they were usually highest in source sites and lowest in pseudosink sites (Figure 4).

DISCUSSION

My results provide several lines of evidence for source-sink metapopulation dynamics in a freshwater fish species, linked to the introduction of a non-native predator. Trout were associated with decreases in YOY recruitment, both among backwater-occupying fry and free-swimming juveniles. The effect of trout presence on *G. vulgaris* size structuring indicates a shift in demographic processes that can best be explained by source-sink dynamics.

Model selection indicated an interaction between the effect of trout invasion and stream width best described *G. vulgaris* fry densities in summer and autumn. Stream width was closely associated with other habitat size variables in the PCA and is therefore a good proxy for habitat size across the riverscape. Fry densities were positively correlated with stream size within trout-free sites in summer, even though these reaches were uniformly small in the context of the overall riverscape. Initial *G. vulgaris* fry densities have been linked to the local densities of adults (Jellyman and McIntosh 2008), and it is possible that very small headwater reaches contained limited habitat for *G. vulgaris* compared to larger reaches, resulting in increases in fry production with stream size. The positive association between fry density and stream

size remained intact in trout-free streams through autumn, suggesting apparent fry survival did not change with increasing stream size in trout-free reaches.

In contrast to most trout-free reaches of the same size, small trout-invaded reaches had few or no fry in summer. This pattern suggests predation by trout had an overriding effect on fry recruitment in small streams. In a field experiment conducted on a small trout-invaded stream in the area, trout rapidly eliminated *G. vulgaris* fry inside backwaters they had access to, whereas backwaters fenced to prevent trout access (but allowing fry emigration) retained many fry (McIntosh et al. 2010). While most trout-free reaches retained fry into autumn, few fry remained in trout-invaded reaches, and mostly occurred in backwaters and side braids that were disconnected from the main channel. Whether or not trout gained access to the backwaters during the course of the summer appears a better predictor of apparent fry survival than stream size in trout-invaded reaches.

Trout presence was the most important predictor of YOY *G. vulgaris* biomass at monitoring sites in each winter survey. This result, together with the patterns of apparent fry survival, indicates trout were the cause of YOY recruitment failures. The presence of large (>100 mm) trout has been linked to the loss of recruits in a congeneric species (McIntosh et al. 1994) and the complete loss of galaxiids from invaded streams both in my study system and other regions of the South Island (Townsend 1996, McIntosh 2000). Furthermore a mesocosm experiment showed large (>150 mm) trout to prey on all sizes of *G. vulgaris* (McIntosh 2000). Trout of this size or larger were present within all sink sites, which also supported the highest biomass of trout. This high predator biomass appears to have depleted all but the largest *G. vulgaris* individuals.

The high densities of fry retained in trout-free reaches, together with the consistently high densities of YOY fish occurring at trout-free monitoring sites, suggest positive net recruitment and therefore positive population growth rates within these reaches, a prerequisite for a demographic source (Pulliam 1996, Diffendorfer 1998). It is unknown how far downstream from the nest *G. vulgaris* fry drift before settling in backwaters, but long distance dispersal is possible for the species (Benzie 1968). Consequently, trout-free populations are likely exporters of passively dispersing fry

into downstream, mostly invaded, reaches. Conversely, it is physically impossible for the invaded reaches to export fry to trout-free reaches upstream.

It may be tempting to think the one-way dispersal of galaxiid fry could lead to a source-sink dynamic in *G. vulgaris* independent of trout. Under this scenario, upstream sites would be natural sources (net exporters of individuals) and downstream sites natural sinks (net importers of individuals) if there were insufficient reciprocal upstream migration of adults (Slack et al. 2004, Hänfling and Weetman 2006), but I think this is unlikely. Adult *G. vulgaris* are potentially highly mobile, rapidly dispersing to re-colonise habitat left vacant after drying disturbance (Davey and Kelly 2007). Moreover, three sink sites that contained adults but never YOY recruits were located on tributaries upstream of the nearest source stream, and must have been sustained by adult immigration from downstream. It is therefore unlikely that a source-sink metapopulation based on one-way dispersal existed in *G. vulgaris* in my study system prior to the introduction of trout.

The four pseudosink sites that retained YOY fish also contained the lowest biomasses of *G. vulgaris* and trout. These patterns suggest the potential for positive *G. vulgaris* population growth, but at a lowered carrying capacity, two defining features of pseudosinks (Pulliam 1996). These reaches were also large, disturbed, or both. Carrying capacity for galaxiids and trout could therefore be limited by flood disturbance, which would reduce invertebrate food resources (Death and Winterbourn 1995, Suren and Jowett 2006). In contrast, greater habitat complexity within the large, often braided pseudosink reaches may enhance *G. vulgaris* survival by enabling selection of different microhabitats than trout (McIntosh et al. 1992, Glova and Sagar 1993, Leprieur et al. 2006). Thus conflicting biotic and abiotic controls at pseudosink sites may enable sporadic positive population growth despite the presence of trout.

If one assumes all trout-invaded reaches where *G. vulgaris* fry survived until autumn within the Broken River network are true pseudosinks, they amount to only 7% of the surveyed riverscape. In contrast, trout-free source reaches comprised only 16%, whereas trout-invaded sink habitat made up 69%. These figures suggest that *G. vulgaris*, while seemingly common across the riverscape as a whole, may in fact be

quite vulnerable to extinction within these networks. If trout were introduced into the trout-free reaches of these streams, galaxiids in both the source and linked sink populations would likely be eliminated (Townsend 1996, McIntosh 2000, McDowall 2006). Only in the pseudosink habitats, where self-recruitment is maintained despite the presence of trout, would *G. vulgaris* populations likely survive over several generations.

As pseudosink habitats tended to have elevated disturbance and supported low numbers of galaxiids, they are also inherently susceptible to local extinction (Dunham and Rieman 1999, Hilderbrand 2003). Demographic modelling of isolated salmonid populations elsewhere suggests that limiting immigration to populations with low carrying capacity can severely increase extinction risk (Hilderbrand 2003). Thus, by removing source populations and consequently isolating pseudosink reaches, invasive predators like trout could drastically reduce the viability of the prey metapopulation despite its apparent size and potentially high patch connectivity, normally earmarks of low extinction risk (Dunham and Rieman 1999, Fagan 2002).

Conservation implications

My findings suggest the viability of *G. vulgaris* populations in New Zealand streams may not be evident from their current size and extent, as much of their distribution comprises trout-induced sink habitat. *Galaxias vulgaris* is not currently considered a conservation priority (Department of Conservation 2004) due in part to its wide distribution and co-occurrence with trout. This case study highlights the challenge of managing populations for which demographic data are difficult or costly to obtain, despite the fact that incorrect management decisions could be made in the absence of such data (Lande 1988, Cooper and Mangel 1999). I recommend that managers of native species threatened by patchy invaders consider whether instances of co-occurrence are in fact invader-driven source-sink metapopulations dependent on refuge populations.

Invasive predators have the potential not only to create sinks within prey metapopulations but also, through continued invasion, to convert old sources into new sinks, potentially destabilising the entire metapopulation. In particular, continual invasion of new freshwater habitats by predatory sport fish, often through illegal

human introductions, is an ongoing process that continues to have negative consequences for aquatic biodiversity around the world (Cambray 2003). It is therefore critical that management effort be directed toward the identification and preservation of invader-free habitat, since these habitat patches may act as linchpins in controlling the persistence of threatened species throughout riverscapes or landscapes. Such fragile metapopulations could in turn be stabilised through the removal of the invader to expand existing invader-free populations (Lintermans 2000). New demographic sources could also be created through translocation of threatened species to invader-free habitats within the landscape (Harig and Fausch 2002), reinforcing metapopulation stability.

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Plate 2: A juvenile *Galaxias paucispondylus* peers from benthic cover (Photo: Angus McIntosh)

Chapter 3

Biotic and abiotic drivers of co-occurrence between introduced trout and native alpine galaxias (*Galaxias paucispondylus*) across New Zealand riverscapes

ABSTRACT

Introduced trout (*Salmo trutta* and *Oncorhynchus mykiss*) can negatively affect the distribution and survival of native non-diadromous galaxiids in New Zealand. Although two galaxiid species, *Galaxias paucispondylus* and *G. vulgaris,* co-occur with trout, it is unknown whether the mechanisms controlling co-occurrence are the same for both species. This study assessed whether trout negatively affect *G. paucispondylus* recruitment, as is the case for *G. vulgaris*, and determined the roles of habitat variability and in determining their distributions. The predatory impact of trout on both galaxiid species was compared using stream manipulation and artificial mesocosm experiments to determine effects of trout size and species identity on galaxiid survival. I assessed how habitat variability and trout presence predict *G. paucispondylus* distributions using logistic regression, and how these factors affect biomass of yearling *G. paucispondylus* recruits through information-theoretic testing of least-squares models. Large trout significantly decreased biomass of both species in the stream manipulation, and both *G. paucispondylus* and *G. vulgaris* were equally vulnerable to predation by either trout species in experimental mesocosms. Trout presence did not significantly predict *G. paucispondylus* landscape-scale distributions, although positive associations with aquatic macrophytes could indicate preference for habitat containing refugia from predation. Biomass of *G. paucispondylus* recruits was highest in small, disturbed reaches where summer low flows provide hydraulic refuge for larvae. The species' apparent dependence on disturbed streams for recruitment could make *G. paucispondylus* vulnerable to future increases in disturbance variability. *Galaxias paucispondylus* distributions appeared restricted by high water temperatures, indicating a potential vulnerability to climate change. While adaptation to disturbed environments may enhance coexistence with invasive predators, shifting environmental stressors could exacerbate the effects of the predators on native populations over time.

INTRODUCTION

There is a pressing need to understand the mechanisms driving invasive predator effects on native prey species in freshwater systems, as the impacts of invasions can be severe (Cambray 2003, Cox and Lima 2006). Hydrologic disturbance (drying and flooding) can ameliorate impacts of introduced predatory fish by preventing their establishment (Moyle and Light 1996a, Fausch et al. 2001), or by lowering their densities and subsequent interactions with native prey (Meffe 1984, Bernardo et al. 2003, Leprieur et al. 2006). By having suitable morphological and behavioural adaptations to local disturbance regimes, prey species may be able to persist in the presence of less well-adapted introduced predators (Meffe 1984, McIntosh 2000). The ability of native prey species to utilise structural cover in complex habitats can also enable co-existence with introduced predators (MacRae and Jackson 2001, Macchi et al. 2007). Prey species may also vary in their ability to avoid predation through their different use of habitat cover (Walls 1995). Thus, contrasting co-occurrence between introduced predators and different native prey species may be the result of differences in each species' adaptation to spatial and temporal habitat variability.

The successful invasion of freshwater habitats in New Zealand by introduced brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum), has resulted in the apparent extirpation of native non-diadromous galaxiid fishes from many places (Townsend 1996, McDowall 2006). However, two species, the Canterbury galaxias (*Galaxias vulgaris* Stokell) and the alpine galaxias (*G. paucispondylus* Stokell), still co-occur with trout in the mountain tributaries of the South Island (McIntosh 2000, Elkington and Charteris 2005). *Galaxias paucispondylus* differs from *G. vulgaris* in that it belongs to a morphological group of small, elongated, non-diadromous galaxiids known as "pencil galaxiids", that appear restricted to cold, fast-flowing streams (McDowall 2000, McDowall 2006). *Galaxias paucispondylus* is also restricted to higher altitude tributaries than *G. vulgaris*, and is numerically dominant when the two species co-occur in hydrologically disturbed streams (Dunn 2003). *Galaxias vulgaris* forms source-sink metapopulations within trout-invaded systems, and emigration from trout-free sources may enable co-occurrence (Chapter 2). Although *G. paucispondylus* appears to be excluded from streams where large trout are common (McIntosh 2000), it is unclear whether trout

predation affects it to the same extent as *G. vulgaris*. Given the different morphologies and environmental responses of the two species, they may have differing vulnerability to trout.

I used three approaches to assess how trout affect *G. paucispondylus* populations, and how this differed from *G. vulgaris*. First, I experimentally assessed the relative predation threat posed by trout to the two species. Second, I assessed whether distributions of large predatory trout or habitat variability affected the overall distributions of *G. paucispondylus* across the landscape of river networks. Third, since trout predation overrides the effect of habitat on *G. vulgaris* recruitment (Chapter 2), I assessed whether trout also affected *G. paucispondylus* recruitment success, or whether habitat conditions were a more likely recruitment driver.

METHODS

Stream predation experiment

To test the differing predatory threats posed by large and small trout on survival of *G. vulgaris* and *G. paucispondylus*, a fish manipulation experiment was conducted in January 2007 on Binser Stream, a small tributary (discharge 0.02-0.05 m^3/s) of the Waimakariri River, South Island, New Zealand, populated by *S. trutta*. The stream was divided into 20 experimental reaches (each 20 m^2) by fences placed across the stream (Figure 1). Each fence consisted of 4 mm-mesh nylon netting attached to 10 mm-mesh plastic backing that was anchored to banks and riverbed by steel posts. Net bases were buried in gravels and cobbles, and gaps between fences and riverbanks sealed with gravel and earth. Reaches averaged 1.8 m wide and 14.5 cm deep, and mean substratum particle size was 77 mm.

Five replicates of four treatments designed to test the effects of varying sizes of trout on the growth-rate (reported in McIntosh et al. 2010) and survival of the galaxiids were established. Treatments included controls with galaxiids only, galaxiids with three small (100-120 mm FL) trout, and galaxiids with one large (150-220 mm FL) trout (the size at which trout can prey on all sizes of *G. vulgaris,* McIntosh 2000). Two densities of the galaxiid only control treatment were used to compare growth rates with and without trout (McIntosh et al. 2010). Reaches were repeatedly

electrofished up to five times to clear resident trout. Young-of-year (YOY) trout (30-50 mm TL), which were hard to catch and not considered to be a predatory threat to galaxiids, were ignored. Once trout were removed, either six or twelve *G. vulgaris* together with six or twelve *G. paucispondylus* were added to each control reach to create high and low density galaxiid-only treatments. Six galaxiids of each species were added to each trout treatment. I added three or six small galaxiids of each species, ranging in size from 45 to 74 mm TL, and three or six large (76 to 110 mm TL) galaxiids, depending on the density treatment. All galaxiids were weighed, measured and tagged subcutaneously on their flanks with non-toxic acrylic paint (following Eldon 1978). Trout were sourced from the experimental site and nearby streams, and tagged in the same way on the adipose fin or at the base of the caudal fin (Whalen and Parrish 1999). Galaxiids were obtained from a stream containing low numbers of small trout, to ensure they were not naïve to trout. Treatments were arranged along the stream using a randomised block design.

Figure 1: Fences dividing experimental reaches on Binser Stream during a fish manipulation predation experiment (Photo: Angus McIntosh).

After three weeks, each pen was electrofished four times to retrieve fish, which were identified, weighed and measured, before being returned to their streams of origin. Galaxiids of both species were sometimes recaptured in different pens from those they had been placed in, indicating some fish had burrowed under the fences. Several unmarked trout were also found in experimental reaches, suggesting imperfect removal, but all experimentally added trout were recaptured in their correct pens. To analyse the results, I adjusted the assignment of treatments to reflect whether they contained large, small or no trout at the end of the experiment. This procedure still produced a balanced design of six replicates of three treatments: no trout control, small trout and large trout. The downstream distance from the centre of each pen to the furthest-upstream fence was calculated as a continuous covariate to enable longitudinal effects on the experimental design to be determined. The effect of trout treatment on galaxiid survival was assessed for each galaxiid species using the proportion of original galaxiid biomass recovered, to take into account the varying numbers of galaxiids in the controls. Proportions were arcsine-square root transformed and tested for treatment and downstream-distance effects using ANCOVA.

Tank mesocosm experiments

Two experiments were conducted during the summer of 2008/2009 in an array of eight circular mesocosms at the University of Canterbury's Cass Field Station to test how cover and trout species (*S. trutta* vs. *O. mykiss*) affected predation on galaxiids. The mesocosms were black plastic cattle-watering tanks (1.24 m base diameter) that provided a wetted surface area of 1.2 m^2 (Figure 2). A clear plastic baffle extended down from a horizontal drainage pipe, bisecting two thirds of the tank. A water jet pointing into the tank on either side of the baffle created a semi-circular flow on each side. This configuration simulated stream flow in a pool, with velocities up to 0.11 m/s near the baffle but with little or no flow at the edges. Water drained though 1 mm mesh windows in the drainage pipe, to maintain a mean water depth of 31 cm. The tanks received water, screened (1 mm mesh) to remove debris and invertebrates, pumped from Grasmere Stream (water temperature 13-16° C), a lake outlet stream containing *S. trutta* and longfin eels (*Anguilla dieffenbachi*).

The first experiment assessed the ability of large (>150 mm FL) *S. trutta* to prey on large and small *G. paucispondylus* in tanks with and without vegetative cover. Vegetative cover in the form of aquatic macrophytes can ameliorate predation by trout on galaxiids in lakes (Stuart-Smith et al. 2007), and was common in stable reaches of the surveyed rivers. I covered the base of each tank with a single layer of gravel (13-75 mm, mean size 45 mm), and planted half the tanks with stands of aquatic macrophytes (*Nasturtium* sp), harvested from Grasmere Stream. I planted 20 l wetted volume of stalks, leaves and roots in the backwater on either side of the baffle (Figure 2), to simulate the marginal macrophyte stands encountered in small, stable streams where *G. paucispondylus* and trout co-occurred.

Figure 2: A mesocosm (1.2 m diameter) used in predation experiments, showing a macrophyte treatment in the *G. paucispondylus* vegetative predation cover experiment. Note the transparent baffle suspended vertically from the centre of the tank. White arrows represent direction of highest velocity water flows in the mesocosm.

To encourage normal foraging behaviour in both galaxiids and trout, I seeded each tank with 400 *Deleatidium* mayflies, abundant and ubiquitous invertebrates that are fed on by both galaxiids and trout in New Zealand streams (Cadwallader 1975a). The resulting density of 250 *Deleatidium* per square metre reflects minimum natural densities recorded in the Waimakariri catchment (P. Jellyman, University of Canterbury, unpublished data). Using a factorial design, I added a single large trout (172-187 mm) to four of the eight tanks, creating treatments of trout only, trout + macrophytes, macrophytes only, no trout + no macrophytes. I ran the experiment twice, reassigning treatments, to obtain 4 replicates for each treatment, blocked by time. Three small (56-75 mm) and three large (82-96 mm) *G. paucispondylus* were added to each tank 16 hours before the trout were added, so that they could acclimatise and adopt normal cover-seeking behaviour. Galaxiids were obtained from nearby Lower Farm Stream, where trout were present in low densities. The experiment ran for 48 hours starting at 11 am and incorporating four crepuscular periods when feeding activity by trout and galaxiids was likely to overlap (Glova et al. 1992).

A second mesocosm experiment compared the effect of trout species (*S. trutta* and *O. mykiss*) on survival of small (YOY or 1+) *G. vulgaris* and *G. paucispondylus* in a more controlled environment than the stream fence manipulation. All mesocosms were given the same gravel cover base as in the first experiment, but two small (111-114 mm), two medium (150-200 mm) and two large (210-270 mm) cobbles were added to provide extra benthic cover. *Deleatidium* mayflies were added as in the first experiment, along with four *G. vulgaris* (58-75 mm) and four *G. paucispondylus* (59-79 mm). One large *S. trutta* (169-187 mm) or one *O. mykiss* (179-195 mm) was added to six of the eight tanks. The trout treatments, with both species of galaxiid in each tank, created a six replicate split-plot design. The two remaining tanks served as trout-free monitoring controls, which were not used in statistical analyses. Trout were added at 11am, 16 hours after the galaxiids and the experiment terminated after 48 hours.

Riverscape distribution surveys

Fish distribution surveys were conducted in three sub-catchment networks or "riverscapes" (*sensu* Fausch et al. 2002) located in the Waimakariri and Rakaia River catchments. Both catchments drain the eastern slopes of the Southern Alps, South Island, and flow into the sea north and south of Christchurch, respectively (Figure 3). The riverscapes were chosen to represent a diversity of streams that contained *G. paucispondylus* and trout, as well as *G. vulgaris*. The Acheron riverscape in the Rakaia catchment, and the Porter and Broken riverscapes in the Waimakariri catchment, all comprised third-order streams and their fish-occupied headwater tributaries.

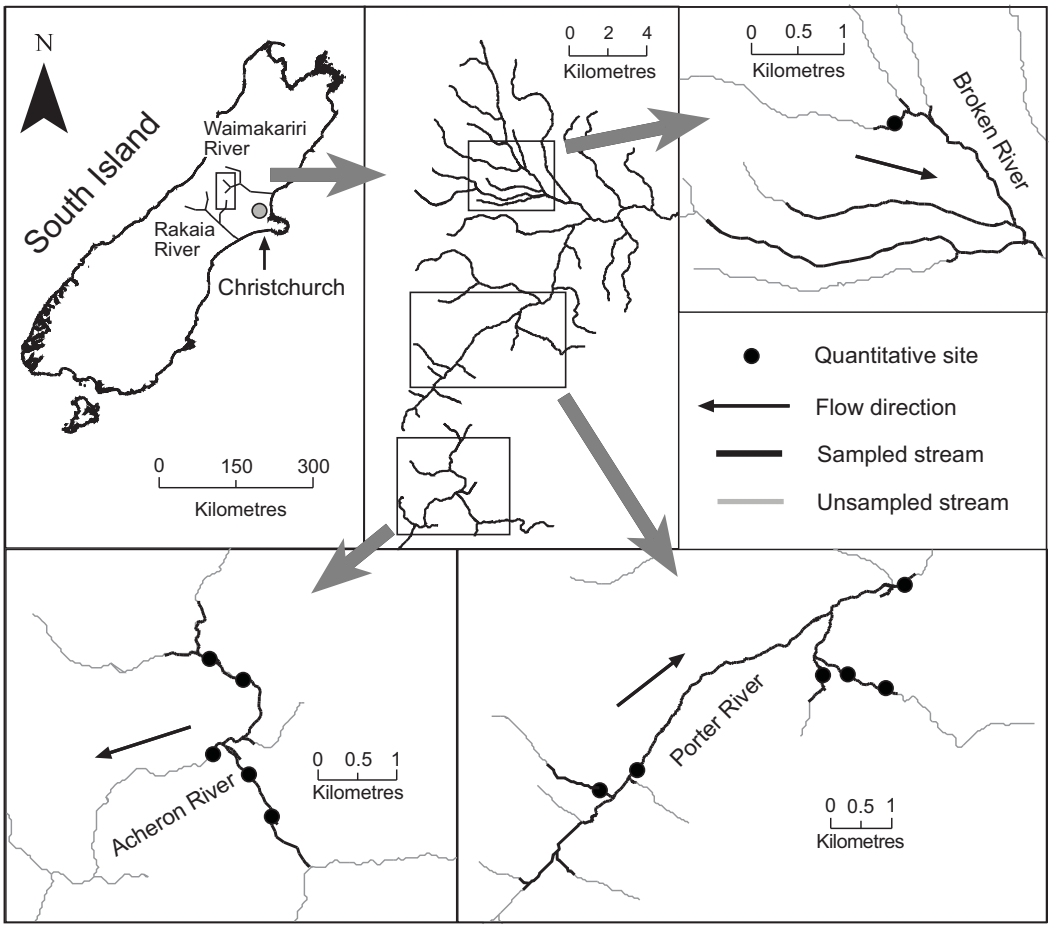

Figure 3: The study riverscapes, inland of Christchurch (grey circle), South Island, New Zealand. The localities and extent of surveyed riverscapes are shown in bold. Quantitative monitoring sites where *G. paucispondylus* was recorded are shown by black circles. These sites were a sub set of monitoring sites located to efficiently capture most habitat variability that occurred across the riverscapes.

Electrofishing surveys were conducted in January to March 2007, with an additional survey in March 2008, at multiple reaches (30-80m length, based on river bends) within each trout-invaded riverscape (22 in the Acheron, 60 in the Porter, 27 in the Broken). Surveys were designed to obtain samples of fish distributions across river networks in a more spatially extensive manner than could be achieved through quantitative sampling, thus achieving better resolution in measuring fish distributions across riverscapes. Three areas, each measuring approximately one meter by two meters, were electrofished within each survey reach. Sampling areas were chosen that contained high levels of instream cover for fish (either from benthic structure or from aquatic macrophytes). Electrofishing was performed using a Kainga EFM 300 backpack electrofisher (NIWA instrument Systems, N.Z.) generating 400-600V pulsed DC current, and was conducted downstream into a push net, the standard practice for catching benthic galaxiids in New Zealand streams (Townsend and Crowl 1991).

The ability of the spot-fishing technique to detect galaxiids and trout was assessed by comparing records at selected sites where quantitative depletion electrofishing was also performed (see below). *Galaxias paucispondylus* was successfully detected at 78% of extensive survey reaches where quantitative electrofishing later confirmed their presence. Spot fishing successfully detected trout at 92% of quantitative sampling sites where they occurred, although large trout (>150 mm FL) were only detected at 44% of quantitative sites where they occurred. Therefore false absences of galaxiids and trout were probably rare in the riverscape survey, but large trout were difficult to detect with this method.

Habitat characteristics were measured at all surveyed reaches. Maximum depth within a reach was recorded to the nearest cm, and the upstream and downstream widths were measured to the nearest 0.1 m. The magnitude of riverbed disturbance visible at the site was assessed according to the River Disturbance Index (Pfankuch 1975), a subjective index that uses characteristics of the upper and middle banks, and riverbed to assign a numerical disturbance rating that correlates strongly to substratum movement caused by flooding (Death and Winterbourn 1994, Greenwood and McIntosh 2008). Aquatic and riparian vegetative cover were assessed within the central 20 m of each surveyed segment. Within each 20 m sub-sample, the

percentages of overhanging and emergent aquatic vegetation covering each bank, and the percentage of the overall riverbed covered by submerged aquatic vegetation, were visually estimated.

Quantititative fish surveys

Quantitative sampling of *G. paucispondylus* populations was conducted in February 2007 at five sites in the Acheron River network, six sites in the Porter River network and one site in the Broken River network (Figure 3). This intensive fish sampling was used to assess the relative effects of habitat and trout biomass on biomass of YOY *G. paucispondylus*. The presence of YOY fish is a good indicator of recruitment success (Driver et al. 2005), and the absence of such recruitment would indicate reduced population viability, which may be in turn be driven by trout (Chapter 2). Because high water temperatures at low altitudes could also limit the distribution of *G. paucispondylus*, sites were selected from a larger set of pilot survey sites after the presence of *G. paucispondylus* had been confirmed. The 20 m long quantitative sites were surveyed using three-pass depletion electrofishing, with stop nets placed upstream and downstream of each site. Fish were measured and weighed before being returned to the stream, and abundances were determined using the Maximum Weighted Likelihood model of Carle and Strub (1978). Biomass per unit area was calculated as the mean weight (g) of each species captured at a site multiplied by abundance and divided by the surface area of the monitoring site. I estimated total numbers of young-of-year (YOY) *G. paucispondylus* separately and calculated their biomass per square metre. YOY were defined as all individuals <60 mm TL (Bonnett 1990). These fish represented a cohort spawned in the previous spring that had survived a backwater-dwelling larval stage to recruit to the stream-dwelling population. River disturbance and vegetative cover were assessed as in the riverscape surveys. Mean width and depth of each site were calculated from measurements made at three points on three transects. I also measured the maximum length of 30 randomly selected substratum particles within each site.

Temperature monitoring

Temperature was recorded hourly at quantitative sampling sites using WT-HR1000 stage-height loggers (Trutrak Ltd, Christchurch, N.Z.) from 2006 to 2008, and with iButton© DS1921 temperature loggers at selected survey sites on all three riverscapes

over the summer of 2007/2008. I used quantitative and riverscape survey data to assess the presence or absence of *G. paucispondylus* at these sites relative to the maximum water temperature recorded in January 2008 (the month where water temperatures reached their annual maximum).

Survey data analyses

The effects of habitat and trout on *G. paucispondylus* populations were assessed at two spatial scales. Using riverscape-scale survey data, the presence of *G. paucispondylus* was modelled as a function of habitat and the presence of large trout, using a generalised logistic regression model. The effect of January maximum water temperature on *G. paucispondylus* presence across all riverscapes, was also assessed at this scale.

At the scale of quantitative survey reaches, I assessed the relative effects of habitat and trout on *G. paucispondylus* recruitment success, by comparing models that predicted YOY biomass using information-theoretic model selection (Burnham and Anderson 2002). Habitat variability at quantitative sites was first summarised using Principal Components Analysis (PCA). The two PCA factors that explained most habitat variability were used as habitat predictor variables. A set of candidate least squares models using habitat and trout biomass as predictors of YOY *G. paucispondylus* were compared using the Akaike Information Criterion (AIC_c) adjusted for small sample sizes (Burnham and Anderson 2002). Candidate models included (1) univariate models with trout presence, PCA 1 or PCA 2 as predictors; (2) additive models with trout and either PCA axis, and (3) additive model with the PCA axes only. To avoid over-parameterisation given my small sample size, I limited models to a maximum of two predictors and did not consider interactions. The AIC, AIC_c and AIC weights were calculated for each model based on its residual sum of squares. The difference between each model's AIC_c and the best (lowest scoring) model's AIC_c, or ΔAIC_c, was calculated (Burnham and Anderson 2002). Models with $|\Delta AIC_c| < 2$ were regarded as being similarly informative to the best model. All biomass data were square root transformed, continuous habitat data were $\log_e$-transformed, and all percentage data were arcsine-square root transformed to meet the required assumptions of normality and homoscedasticity. Statistical analyses were performed in Statistica 8 (Statsoft 2007).

RESULTS

Stream manipulation experiment

Large trout treatment had a significant negative effect on recaptured biomass of both *G. vulgaris* and *G. paucispondylus* in the fenced stream experiment (Table 1). The proportion of original *G. vulgaris* biomass remaining was significantly less in large trout treatments than in trout-free treatments (Post-hoc Tukey HSD: $p < 0.05$, Figure 4a), and the proportion of original *G. paucispondylus* biomass remaining was significantly less in large trout treatments than in small trout treatments (Figure 4b). Of the galaxiids recovered, 13% of *G. vulgaris* (total recaptured n = 52) and 31% of *G. paucispondylus* (total recaptured n = 35) were found in different pens to those in which they had been placed, indicating *G. paucispondylus* had burrowed under fences at a higher rate than *G. vulgaris*.

Table 1: ANCOVAs testing the difference in proportions of initial stocked biomass of *G. vulgaris* and *G. paucispondylus* remaining within fenced segments of Binser Stream containing small, large or no trout, using longitudinal distance of pens from upstream end of the array of pens as a continuous covariate.

Effect	df	F	p
G. vulgaris			
trout size treatment	2	4.16	0.04
distance	1	0.67	0.42
error	14		
G. paucispondylus			
Trout size treatment	2	4.89	0.02
distance	1	0.12	0.73
error	14		

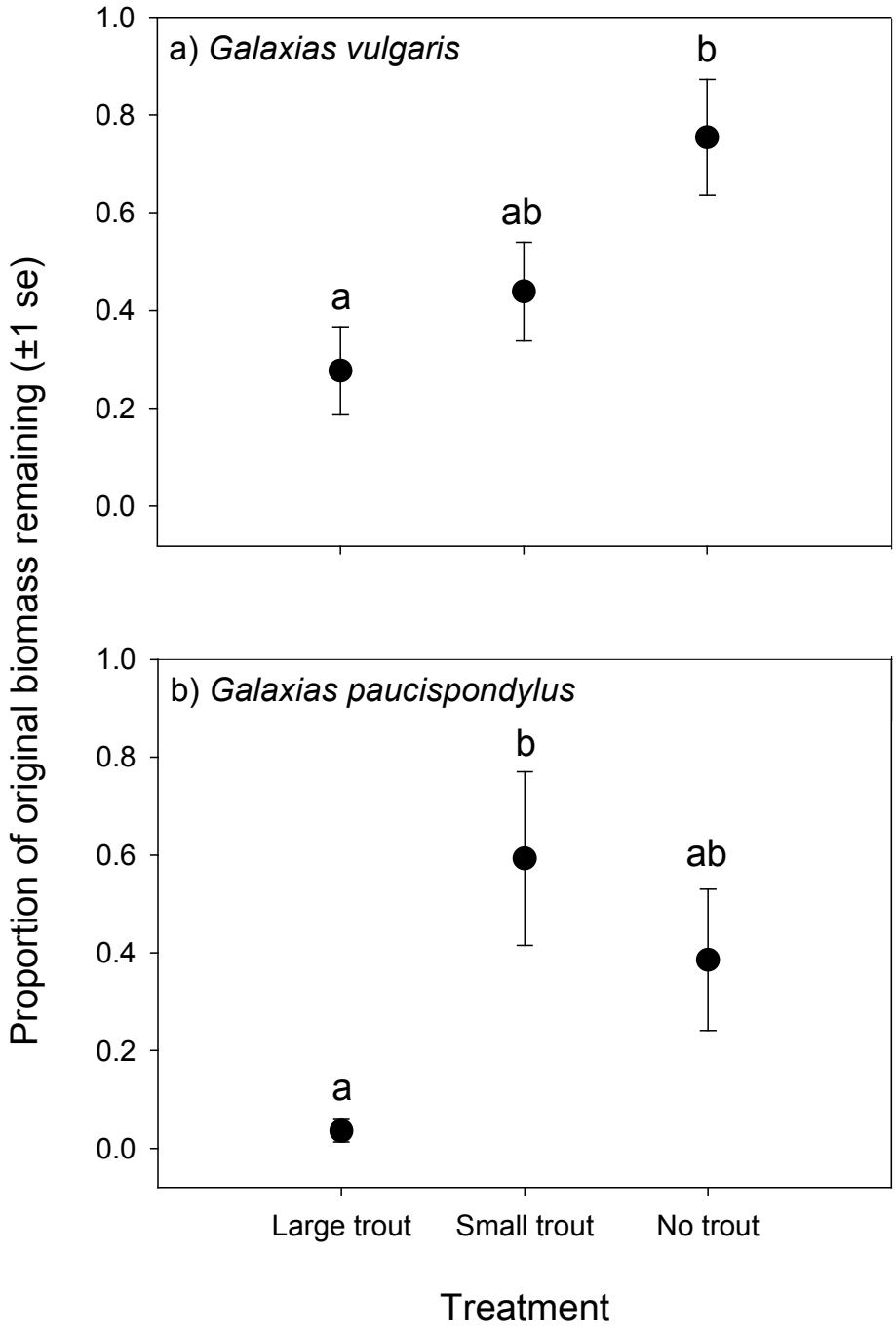

Figure 4: Proportions (mean ±1 standard error) of original stocked biomass of a) *Galaxias vulgaris*, and b) *G. paucispondylus* remaining in experimental reaches with different sizes of trout at conclusion of the stream-manipulation experiment in Binser Stream. Large trout treatments contained one trout 150-220 mm FL, while small trout treatments contained 3 trout 100-120 mm FL. Significantly different proportions (Tukey HSD test, $p < 0.05$) are indicated by different letters.

Mesocosm experiments

In the vegetative cover experiment, large trout caused significant mortality of galaxiids in both the vegetated and non-vegetated tanks, whereas no galaxiids were lost from the controls (Table 2, Figure 5). There was a significant interaction with time (Table 2), because galaxiid mortality was low in the first run of the vegetated trout treatments, but high in the second run. Although eight *G. paucispondylus* and three *G. vulgaris* were consumed in the multi-species predation experiment, there was no significant effect of trout species identity or galaxiid species identity on galaxiid mortality rates (Table 2). No galaxiids were lost from the control mesocosms that accompanied this experiment.

Table 2: (a) Factorial ANOVA testing the difference in survival of *G. paucispondylus* in vegetated and non-vegetated mesocosms with and without a single large (>150 mm) trout; (b) nested ANOVA testing the difference in survival between small (<75 mm) *G. vulgaris* and *G. paucispondylus* across treatments containing a single large brown trout (*S. trutta*) or rainbow trout (*O. mykiss*), nested within the effect of trout species on the survival of all galaxiids within mesocosms.

Effect	df	F	p
a) Factorial ANOVA			
Effect of vegetation mediating trout impacts on overall survival			
treatment	3	35.41	<0.0001
time	1	7.23	0.03
treatment x time	3	15.20	0.001
error	8		
b) Nested ANOVA			
Effect of trout species on overall and individual galaxiid species survival			
trout species	1	0.50	0.49
galaxiid species (trout species)	2	0.72	0.51
error	8		

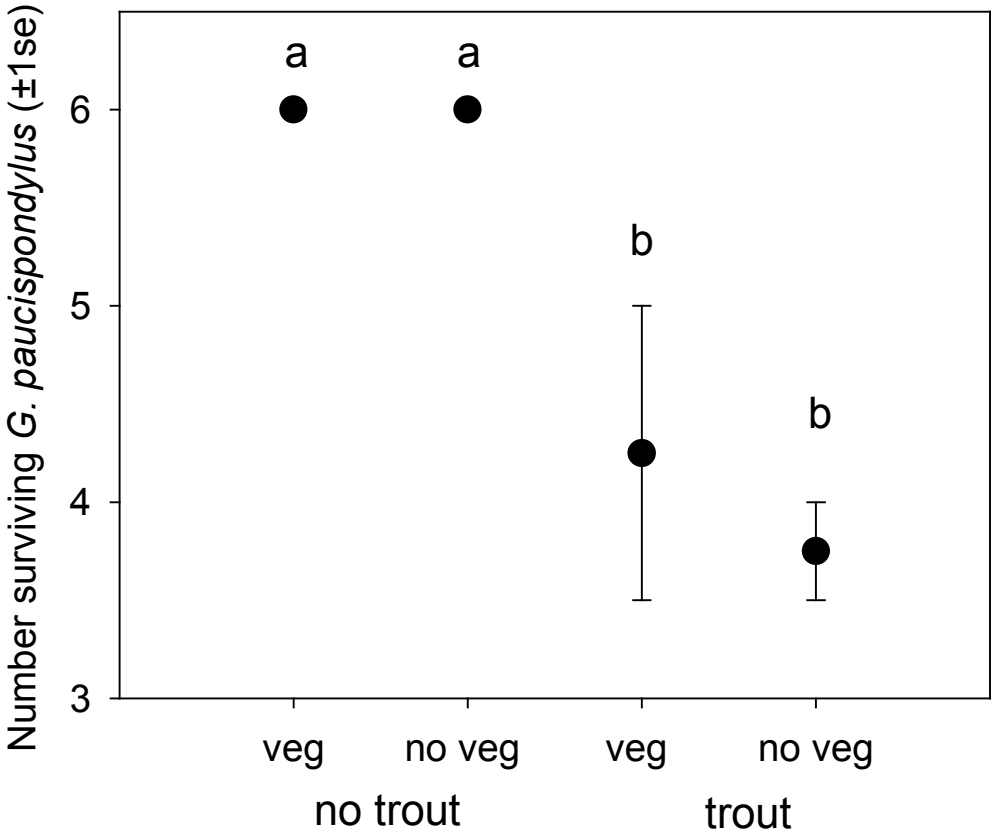

Figure 5: Number (mean ±1 standard error) of *G. paucispondylus* remaining across trout and cover treatments (vegetative cover or no vegetative cover), in a mesocosm experiment assessing the effect of emergent macrophytes on predation of *G. paucispondylus* by trout. Significant differences indicated by different letters.

Field distributions of *Galaxias paucispondylus*

Presence of *G. paucispondylus* at riverscape survey sites was positively associated with altitude and emergent aquatic vegetative cover and was negatively associated with overhanging vegetative cover in the logistic regression model (Table 3). While overhanging vegetative cover was often present at survey reaches, less than 12% of reaches contained more than 50% emergent vegetative cover (Table 4), indicating this cover type was a relatively scarce feature that often predicted *G. paucispondylus* presence. At quantitative and riverscape survey sites where temperature had been monitored, *G. paucispondylus* was recorded only where January maximum temperature was less than 18ºC (Figure 6).

Table 3. Effects of habitat and presence of large trout on *G. paucispondylus* occurrence based on a logistic regression model. Significant effects in bold.

Effect	Wald Statistic	Estimate	p
depth	0.75	-0.75	0.39
disturbance	0.86	1.67	0.35
altitude	**8.04**	**14.49**	**0.005**
stream width	0.28	0.39	0.59
% emergent veg.	**10.27**	**4.02**	**0.001**
% submerged veg.	1.16	1.83	0.28
% overhanging veg.	**7.27**	**-4.07**	**0.007**
large trout presence	1.25	-0.54	0.26

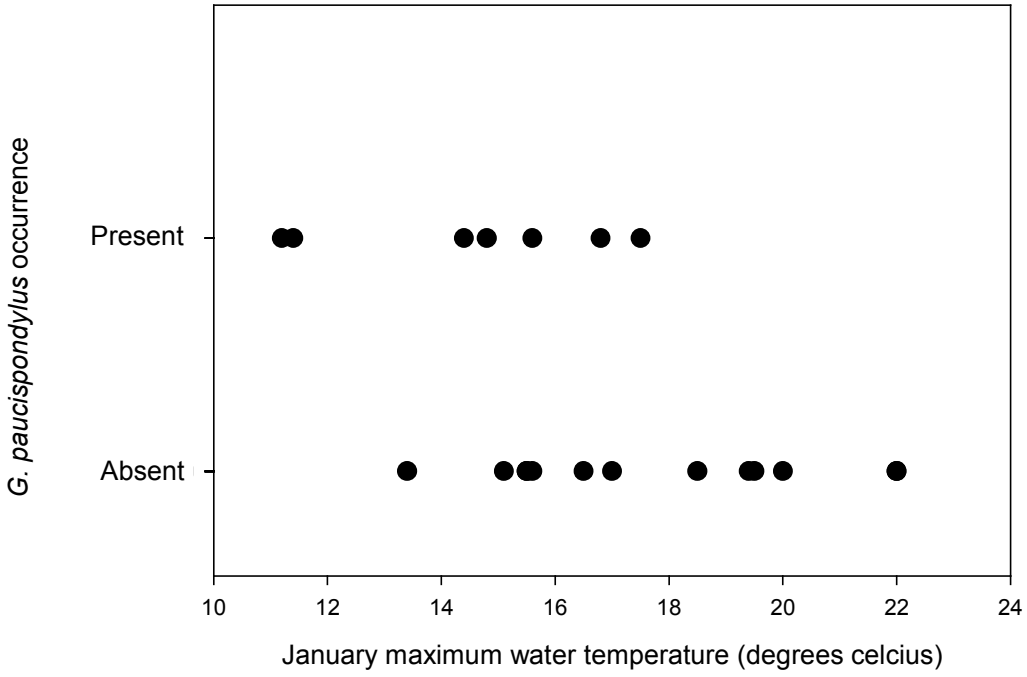

Figure 6: Presence and absence of *G. paucispondylus* along a gradient of maximum January 2008 water temperature at 18 sites where temperature was monitored within the Acheron, Broken and Porter riverscapes (Figure 1).

Table 4: Summary statistics of the prevalence of three types of vegetative cover recorded at 101 surveyed reaches across three riverscapes. Percentage cover refers to the central 20 m of a given survey reach, which varied in total length to fit upstream and downstream channel meanders.

Vegetative cover type	Percentage presence across all reaches	Percentage sites where cover exceeded 50%	Mean percentage cover per reach where present
Emergent vegetative cover	40%	12%	35%
Submerged vegetative cover	45%	6%	30%
Overhanging vegetative cover	71%	30%	43%

AIC_c model testing of YOY *G. paucispondylus* biomass drivers showed a model with only habitat PCA 2 as a predictive variable was best (Table 5). Habitat PCA2 described 28% of total habitat variability and was positively associated with depth and width, and negatively associated with disturbance (Table 6). PCA 2 was negatively associated with on YOY biomass (parameter estimate: -0.18; 95% confidence limits: -0.29, -0.06). These analyses indicate that YOY *G. paucispondylus* abundance was highest in small, shallow streams with elevated bed disturbance.

Table 5: Selection of linear models to describe *G. paucispondylus* YOY biomass through Δ AIC_c analysis. Best models had a Δ AIC_c > -2. PCA factors 1 and 2 summarise habitat variability at sampling sites (see Table 5).

Model	Model Predictors	K	RSS	AIC	AIC_c	Δ AIC_c	AIC w
a)	PCA 2	3	0.43	-29.70	-26.27	0.00	0.75
b)	PCA 1 + PCA 2	4	0.34	-30.09	-23.47	2.84	0.18
c)	Trout biomass + PCA 2	4	0.42	-27.81	-21.14	5.13	0.06

Table 6: Factor correlations with habitat variables in a principal component analysis summarising habitat variability at 12 quantitative fishing sites distributed across three sampled sub-catchments.

	PCA 1	PCA 2
Eigenvalue	3.39	1.96
% of total variance explained	48.43	28.07
Habitat variables		
Depth	0.19	0.95
Width	0.27	0.87
Substrate size	0.63	0.24
Disturbance	0.82	-0.44
% emergent vegetation	-0.95	0.03
% submerged vegetation	-0.93	0.07
% overhanging vegetation	-0.71	0.17

DISCUSSION

The coexistence of predator and prey species in aquatic ecosystems is driven by a suite of biotic and abiotic drivers (Jackson et al. 2001). Habitat heterogeneity can mediate spatial interactions of predators and prey, (MacRae and Jackson 2001, Schneider 2001), as can habitat disturbance (Lancaster 1996, Nyström and McIntosh 2003). My results indicate a complex spatial and biotic interaction between *G. paucispondylus* and trout, in which predation could be important, but is not the sole driver of the galaxiid's distributions. Because anti-predator behaviour and morphological adaptations vary among related species, their vulnerability to the same predatory species may vary (Edge et al. 1993, Walls 1995, Relyea 2001). The combined experimental and field evidence indicates *G. paucispondylus*' use of habitat influenced predator-prey interactions, resulting in co-occurrence patterns between this species and trout that are fundamentally different from those seen between trout and *G. vulgaris*.

The field and mesocosm experiments demonstrated both *G. paucispondylus* and *G. vulgaris* were vulnerable to large trout, regardless of the trout species involved. The

number of *G. paucispondylus* that moved between treatments in the stream manipulation suggests emigration as well as mortality contributed to the low numbers of *G. paucispondylus* retrieved from both trout-free and large trout treatments. In contrast, the limited movement of *G. vulgaris* and high remaining biomass in trout-free treatments suggests predation primarily drove losses of *G. vulgaris* from large trout treatments. The combined experimental results nonetheless confirm the threat posed by large trout to *G. paucispondylus*, and indicate the lack of co-occurrence between both galaxiid species and large trout previously reported (McIntosh 2000) were driven at least in part by predation.

Given the experimental results, one might have expected predation by large trout to structure field *G. paucispondylus* populations, as they do *G. vulgaris* (Chapter 2). Nevertheless, no models including trout biomass explained *G. paucispondylus* juvenile recruitment better than a model using only habitat, and *G. paucispondylus* occurrence at the riverscape scale was not significantly associated with the presence or absence of large trout. These results indicate habitat could be a stronger driver of *G. paucispondylus* population dynamics in natural ecosystems, but does not rule out an interaction between trout and habitat that I did not have the power to detect.

Although absence of large trout was not a significant predictor of *G. paucispondylus* occurrence across riverscapes, it may also have been affected by my spot-fishing technique, which often failed to detect large trout in a surveyed reach. Moreover, occurrence of *G. paucispondylus* was positively associated with emergent macrophyte cover, and this may indicate a preference for habitats that provide refuge from trout. Emergent macrophytes (*Nasturtium* and *Mimulus*) were especially common in the stable tributaries of the Acheron riverscape, and dense growths at the margins of runs and pools often contained *G. paucispondylus* when electrofished. Similarly, macrophytes protected the golden galaxias (*Galaxias auratus* Johnston) from predation by introduced trout in a Tasmanian lake (Stuart-Smith et al. 2007). Although the mesocosm experiment that assessed the ability of these plants to mediate trout predation did not detect a significant ameliorating effect of macrophyte cover on rates of trout predation, the ability of *G. paucispondylus* to burrow into substrata to avoid drought disturbance (Dunn 2003) may enhance its ability to utilise such cover to avoid predation. The narrow, elongated shape of *G. paucispondylus* may facilitate use

of interstitial cover beneath vegetation or in the streambed. The large proportion of *G. paucispondylus* that burrowed under fences in the stream manipulation experiment relative to *G. vulgaris* further indicates superior ability to avoid predation through burrowing, compared to the more robust *G. vulgaris*.

The heightened ability of *G. paucispondylus* to use benthic cover may be especially critical to its survival during early development. Fry (post-larval YOY fish, *sensu* Jellyman and McIntosh 2008) of both *G. vulgaris* and *G. paucispondylus* accumulate in backwaters after hatching, before moving into the main channel as their swimming ability increases (Jellyman and McIntosh 2008). *Galaxias paucispondylus* fry are more agile and more benthic in their behaviour than those of *G. vulgaris* during the backwater-dwelling stage (Dunn 2003, Jellyman and McIntosh 2008), making them potentially less vulnerable to trout predation. *Galaxias vulgaris* fry appear to suffer high trout-induced mortality in backwaters (McIntosh et al. 2010, Chapter 2), rendering most trout-invaded reaches demographic sinks for the species (Chapter 2). In contrast, *G. paucispondylus* fry may be able to actively avoid trout predation in backwaters, so that habitat factors like backwater availability could be stronger drivers of recruitment success than the presence of trout.

Juvenile recruitment of *Galaxias paucispondylus* was highest in small, shallow sites with low bed stability. These sites were permanent upwelling reaches within streams with severe flooding and drying regimes. These upwelling zones may provide the best substrate for spawning and rearing young, as the highly porous gravels could shelter eggs and larvae beneath the surface. The shallow, slow summer flows of cold upwelling water in these reaches also make them excellent refugia for all age classes, as their seasonal exposure to floods and extreme low flows make them marginal habitat for trout (McIntosh 2000, Dunn 2003). Furthermore, the availability of interstitial spaces in the gravel of upwelling zones may provide heightened benthic cover from those trout that do penetrate into these reaches. The specific habitat characteristics of these shallow streams that enable them to act as demographic sources for *G. paucispondylus* (and possibly other pencil-shaped galaxiids) in trout-invaded riverscapes deserve further investigation. The abundance of juveniles in such hydrologically disturbed sites varies greatly from generation to generation (Dunn 2003), indicating that recruitment success depends on the timing and severity of such

disturbances. Consequently, although these sites may have provided optimal recruitment conditions during my study, they may not provide consistently suitable habitat for these species.

If hydrologically disturbed streams act as demographic sources for *G. paucispondylus*, populations occupying them risk becoming unstable and losing their source status if flood-disturbance regimes become more variable (Golinski et al. 2008). Consequently, habitat stochasticity may affect *G. paucispondylus* populations negatively, while at the same time mediating the negative effects of trout. This dichotomy appears central to the population dynamics of *G. paucispondylus*, and deserves further investigation. Research is also needed to ascertain whether competition between *G. paucispondylus* and *G. vulgaris* affect recruitment in either species, and whether indirect food-web effects of trout impact the health of *G. paucispondylus* populations and ultimately their distribution patterns (McDowall 2006).

A correlate of *G. paucispondylus* distribution that likely functioned independently of trout or other galaxiids was altitude. Presence of *Galaxias paucispondylus* across riverscapes was positively predicted by altitude, and this relationship was probably temperature-related. Mean and maximum water temperatures tend to decrease with altitude in mountain streams (Danehy et al. 2005), and thermal thresholds are a well established limiting factor in stream fish distributions (Rosenfeld et al. 2001, Coleman and Fausch 2007). *Galaxias paucispondylus* appears to be limited to high altitude streams through sensitivity to high water temperatures (Dunn 2003), and I found it was absent at sites where summer temperatures peaked above 18ºC. Summer temperature could therefore act as a catchment-scale filter (sensu Malmqvist 2002) that restricts *G. paucispondylus* distributions across riverscapes, and can override effects of local habitat variability or trout.

Temperatures in the South Island are predicted to increase up to 2.5ºC in the next century (Ministry for the Environment 2007), and could result in a contraction of the altitudinal range of *G. paucispondylus*, while trout populations may expand further into high altitude reaches (Scott and Poynter 1991), especially if disturbances become more benign. Such altitudinal range contractions in *G. paucispondylus* could increase

population vulnerability, while increased encounter rates with trout expanding into these headwaters could intensify interactions in reaches where cold temperatures currently make them marginal habitats for trout. Increased water temperatures heighten competitive dominance by warm-water specialist white-spotted char over cold-water specialist Dolly Varden char in Japanese streams (Townsend et al. 2008). The combination of range restrictions and increased encounter rates with invasive salmonids compound the extinction risk facing threatened native salmonids in North America (Peterson et al. 2008, Fausch et al. 2009). The worsening of these environmental stressors may therefore decrease the viability of *G. paucispondylus* populations.

In a dynamic environment, the relative importance of stochastic environmental and deterministic biological processes in driving interspecific interactions will change over time (Strange et al. 1993). Species that have physical adaptations to abiotic stressors that pre-adapt them to better handle biotic stressors like predation will benefit in terms of overall fitness (Garcia et al. 2009), making them more robust to such shifts in ecosystem processes. The ability to react appropriately to invasive predators can be crucial for survival of native species in freshwater environments (Cox and Lima 2006). An improved understanding of how morphological and behavioural adaptations allow native species to cope with invaders is therefore crucial to our ability to predict the outcome of invasions. While *G. paucispondylus* appears to possess morphological traits and habitat preferences that ameliorate the impact of trout at present, there are still many unknowns as to how environmental variability over time will affect these interactions. By monitoring predator-prey interactions over extended timescales, we may gain further insight into how biotic and abiotic factors interact to drive coexistence.

ACKNOWLEGMENTS

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Plate 3: A large rainbow trout (*Oncorhynchus mykiss*) in a stable spring stream (Photo: Angus McIntosh)

Chapter 4

Location of demographic sources affects distributions of a vulnerable native fish in invaded river networks

ABSTRACT

Invasive predators negatively affect native prey to varying degrees across landscapes, and spatial configuration of invader-free refugia may affect prey distributions across the invaded landscape. In New Zealand, introduced brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) create source-sink dynamics in native *Galaxias vulgaris* populations, and their co-occurrence with trout may be driven by propagule pressure of immigrants from trout-free reaches. I investigated how network configuration of trout-free source populations affected the distribution of *G. vulgaris* across trout-invaded riverscapes. Using quantitative biomass surveys and spatially extensive presence-absence surveys across trout-invaded river networks, the interaction of habitat variability and location relative to sources in limiting distributions of *G. vulgaris* was assessed. *Galaxias vulgaris* biomass at sink sites downstream of trout barriers decreased with increasing distance to the nearest barrier. The maximum distance to barriers at which *G. vulgaris* occurred in the riverscape was limited, so that galaxiids were excluded from small and stable streams far from sources. Large trout (i.e. >150 mm FL), which represent a known predatory threat to galaxiid survival, occurred in high densities at stable sites all year round and were seasonally excluded from sites disturbed by flooding. Large streams probably provide increased refugia for galaxiids to avoid predation from trout, but restricted habitat availability and hydrological stability may act synergistically to extirpate *G. vulgaris* from small streams that are too far from sources to receive regular immigrants. The interaction between propagule pressure and habitat configuration in mediating effects of trout on *G. vulgaris* distributions indicates habitat can affect predator-prey interactions in a spatially explicit manner. My findings suggest that creating new invader-free source habitat could enhance co-occurrence in nearby invader-occupied reaches. Adding source habitat in sink streams far from existing sources, and ensuring barriers that prevent future invasion can also allow native fish dispersal between sources and sinks will maximise the conservation gains across invaded riverscapes.

INTRODUCTION

Biological invasions have had a profound negative effect on biodiversity worldwide (Vitousek et al. 1996, Clavero and García-Berthou 2005, Ricciardi 2007). Invasive predators in particular are capable of depleting local taxonomic diversity (Witte et al. 1992, Donlan and Wilcox 2008), although habitat heterogeneity can ameliorate predator impacts by creating refugia for prey species (Lancaster 1996, Kauffman et al. 2007). Habitat heterogeneity can also mediate predator impacts limiting the spread of invasion (Byers 2002) or by facilitating their spread (Didham et al. 2005). In ecosystems where invasion by a predator is patchy, but invader predation pressure on a prey species is high, the prey species may form source-sink metapopulations in the invaded landscape (Basse and McLennan 2003, Chapter 2). The distance to the nearest source patch may affect persistence of prey populations within sink patches, as propagule pressure can decrease with increasing distance from a source (Nol et al. 2005, Meats et al. 2008). I assessed whether the spatial configuration of invader-free sources affected occupancy of invaded sink habitat by the prey species within river networks.

In riverine ecosystems, where dispersal is restricted to a linear path along a dendritic network, distance to demographic sources can be crucial for population viability (Fagan 2002, Eikaas and McIntosh 2006). Consequently, distance to sources may affect the ability of aquatic prey species to persist in sink stream habitat occupied by predatory invaders. Because fish distributions in streams are driven by habitat variability operating at multiple scales, analysis of their distributions relative to sources must be conducted at scales that can detect those interactions (Schlosser 1995, Labbe and Fausch 2000, Fausch et al. 2002). By sampling the "riverscape" at a scale that captures both habitat variability and the spatial context of that variability, the interactive effect of locality and habitat on species distributions can be assessed (Fausch et al. 2002).

I investigated two riverscapes in New Zealand that are invaded by brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum). These species were introduced for angling in the late 1800s, and pose a predatory threat to a group of endemic non-diadromous galaxiid fish species (McDowall 2000, McDowall 2006).

One particular species, the Canterbury galaxias (*Galaxias vulgaris* Stokell), appears to form source-sink metapopulations within trout-invaded riverscapes, where most trout-invaded habitat is a demographic sink for the galaxiid (Chapter 2). Source populations of *G. vulgaris* persist in tributaries above barriers to trout invasion. I surveyed the distributions of *G. vulgaris* across the trout-invaded riverscape to assess how distance to sources affected occurrence patterns in sink habitats.

While decreasing immigration rates may limit the maximum distance *G. vulgaris* could occur from a source, the effect may be offset by local habitat. Variability in environmental disturbance can influence predator impacts, by limiting their distribution and therefore encounter rates with potential prey species (Leprieur et al. 2006, Maret et al. 2006). Large trout in particular are a known predatory threat to *G. vulgaris*, and their riverscape distribution may be limited by flood-related habitat disturbance (McIntosh 2000). Habitat heterogeneity at the stream-reach scale may also enhance species co-existence (Angermeier and Schlosser 1989). Galaxiids avoid trout through microhabitat partitioning (McIntosh et al. 1992, Glova and Sagar 1993), and variable river geomorphology could facilitate habitat segregation. Availability of structural cover may also enhance avoidance of trout (Stuart-Smith et al. 2007, Chapter 3). To evaluate the interaction between immigrant propagule pressure and local habitat in affecting occurrence within sinks, I determined whether *G. vulgaris* was limited in the distance from a source it could occur along various habitat gradients.

METHODS

Study area

The study was undertaken in two sub-catchments of the upper Waimakariri River, draining the eastern slopes of the Southern Alps, South Island, New Zealand (Figure 1). The sub-catchments (riverscapes) included four tributaries of the upper Broken River and three tributaries of the upper Porter River. These were habitat-diverse riverscapes where both trout and galaxiids occurred (Jellyman and McIntosh 2008). A principal cause of stream-habitat heterogeneity in the systems was flood-driven disturbance. In New Zealand such disturbance can be of high magnitude and unpredictable in mountain-runoff tributaries, or low in tributaries with primarily

groundwater sources like springs (Jowett and Duncan 1990). Five trout-free source tributaries for *G. vulgaris* were located in these riverscapes, which were protected from trout invasion by waterfalls, artificial culverts, or seasonally drying reaches that restricted trout movement.

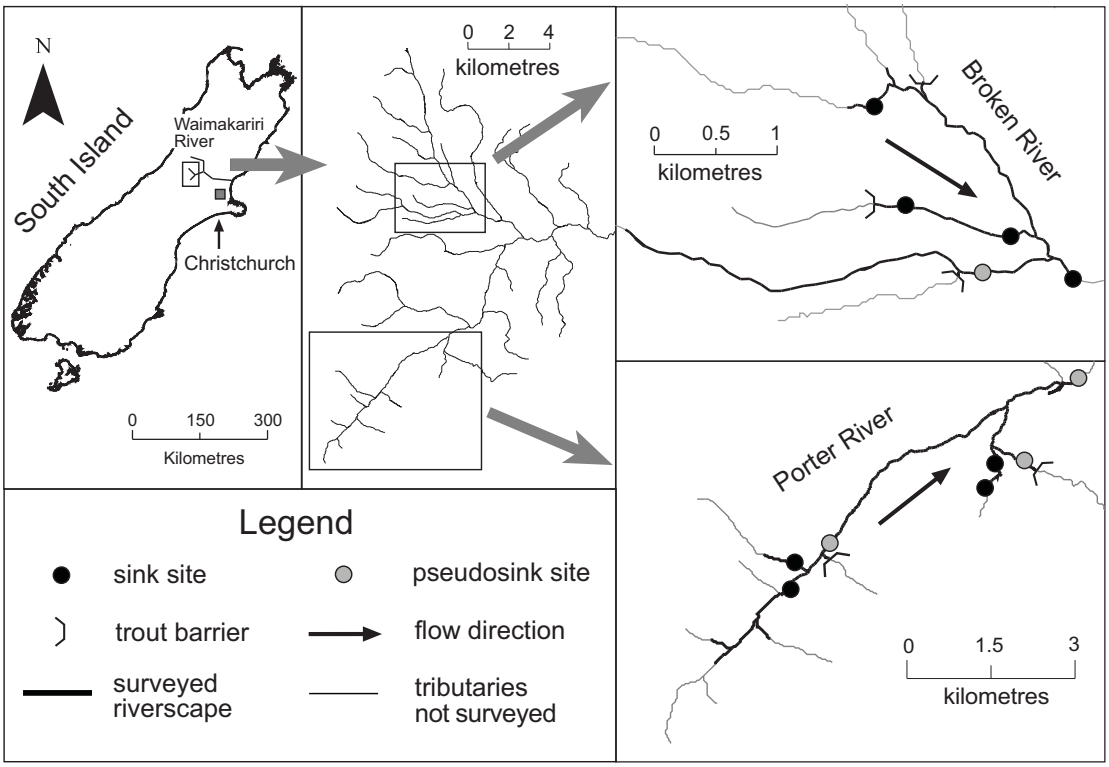

Figure 1: Map of the study area, inland of Christchurch, South Island, New Zealand. The locality and extent of surveyed riverscapes (bold), the location barriers to trout invasion, and the location of sink and pseudosink quantitative monitoring sites are shown. Pseudosink sites displayed limited local recruitment of *G. vulgaris*, so that local populations were likely not dependent solely on immigration from sources to persist over time.

Riverscape distribution surveys

Surveys were conducted on both riverscapes in the austral winter (August 2006) and summer (February 2007), with a short follow-up survey in March 2008 added to the summer dataset to expand the range of habitats sampled. Flow variability on major tributaries was monitored using WT-HR1000 stage-height loggers (Trutrak Ltd, Christchurch, N.Z.) throughout the course of the study. Winter conditions were characterised by low water temperatures and some hydrologic disturbance, with several small floods occurring up to and during the surveys. Summer conditions, in

contrast, were characterised by more stable, steadily declining river flows before and during the survey (Figure 2).

The tributary network of each riverscape was continuously mapped using a Trimble© GEO-XM hand-held geographic positioning system, by plotting the centre of the main channel every 40-80 m, adjusting the spacing between waypoints to match major bends in the river. The waypoints (differentially corrected to a horizontal accuracy of two to ten metres) were used as nodes to build a dendritic river network for each riverscape, using the Geographic Information System ArcGIS 9.1 (ESRI 2005). The portions of river between each node became survey reaches within the riverscape.

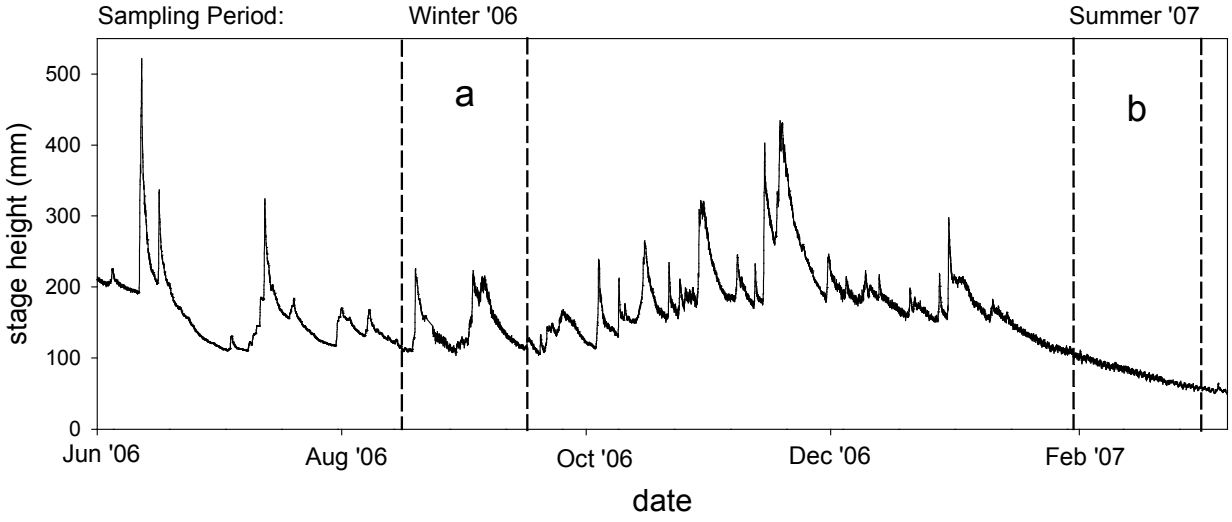

Figure 2: Flow variability measured by stage height on the mainstem of the Porter River over the course of the study. Vertical lines indicate the start and end dates for field sampling in winter 2006 (a) and summer 2007 (b).

Electrofishing surveys were conducted at multiple reaches within each river network. In total 84 reaches in winter and 80 reaches in summer were surveyed. These were spread across 15.4 km of contiguous river segments in the Porter riverscape and 8.7 km in the Broken riverscape (Figure 1). Within each surveyed reach, three sampling areas, each measuring approximately one metre by two metres, were selected. This sub-sampling approach was chosen to maximise sampling efficiency and thereby the total number of reaches that could be surveyed across the riverscape. Sampling areas

were chosen that contained high levels of instream cover for fish (either from benthic structure or from aquatic macrophytes) and where possible were divided between riffles, runs and pools within the reach. However, because riffles dominated most survey reaches, all three habitat types were not always represented. Electrofishing was performed using a Kainga EFM 300 backpack electrofisher (NIWA instrument Systems, N.Z.) generating 400-600 V pulsed DC current. Electrofishing was conducted downstream into a push net, which is standard practice for catching benthic galaxiids in New Zealand (Townsend and Crowl 1991, McIntosh et al. 1994). All captured fish were identified to species and their lengths measured (nearest 1 mm), before being returned to the survey reach. All native fish were measured to total length (TL), while trout were measured to fork length (FL).

The ability of the spot-fishing technique to detect galaxiids and trout was assessed by comparing records at selected sites where quantitative depletion electrofishing was also performed (see below). *Galaxias vulgaris* was successfully detected at 72% of survey reaches where quantitative electrofishing later confirmed their presence. At the sites where detection failed, *G. vulgaris* densities (<0.03 fish/m^2) were an order of magnitude lower than the species' mean density across all sampling sites where they occurred (0.22 fish/m^2). Spot fishing successfully detected trout at 100% of quantitative sites where they occurred, although large trout (>150 mm) were only successfully detected at 62% of quantitative sites. Therefore while false absences of *G. vulgaris* were probably rare and only occurred where densities were extremely low, false absences of large trout were likely more common. This trade-off was deemed satisfactory, as the aim of the qualitative sampling was to determine riverscape-scale distributions of both trout and galaxiids.

Habitat characteristics were measured at all surveyed reaches. The maximum depth within the segment was recorded to the nearest cm, while the upstream and downstream widths (taken at the GPS nodes) were measured to the nearest 0.1 m. The magnitude of riverbed disturbance visible at the site was assessed according to the River Disturbance Index (Pfankuch 1975), a subjective index that uses upper bank, middle bank and riverbed characteristics to assign a numerical disturbance rating that correlates strongly to substratum movement caused by flooding (Death and Winterbourn 1994, Greenwood and McIntosh 2008). Aquatic and riparian vegetative

cover was assessed within the central 20 m of each surveyed segment. Within each 20 m sub-sample, the percentages of overhanging and emergent aquatic vegetation covering each bank, as well as the percentage of the overall riverbed covered by submerged aquatic vegetation, were estimated. Distances between surveyed reaches and the nearest barrier, which occurred both upstream and downstream in the river network, were calculated in ArcGIS by creating a network dataset based on the digitised riverscapes and using the Closest Facility tool in the Network Analyst toolkit.

Quantitative monitoring sites

In addition to the riverscape surveys, twelve quantitative fish monitoring sites were established in trout-invaded reaches on the mainstems and selected tributaries within both riverscapes (Figure 1), and were surveyed in winter 2006 and summer 2007. These sites added a second scale of sampling, which allowed biomass of galaxiids and trout to be assessed at different distances from sources. Sites were classified as either sinks (n = 8) or pseudosinks (n = 4) based on the demographic characteristics of *G. vulgaris* collected at each site. Classification was based on criteria established in Chapter 2, where sinks were sites lacking evidence of local recruitment. Pseudosink habitat, where local recruitment appeared to occur at low carrying capacity, was relatively rare within the trout-invaded riverscape (Chapter 2).

Monitoring sites were 20 m long, and surveyed in winter and summer using 3-pass depletion electrofishing, with stop nets placed upstream and downstream of each site. Fish were measured and weighed before being returned, and numbers were estimated using the Maximum Weighted Likelihood model of Carle and Strub (1978). Biomass per unit area was calculated as the mean weight (g) of each species captured at a site multiplied by the estimated number and divided by the surface area of the monitoring site. I separately estimated the total number of large (>150 mm FL) trout and calculated biomasses based on the mean weight of all fish in this size class captured per site. River disturbance and vegetative cover were assessed in the same way as the riverscape surveys. In addition widths were measured on three transects at each site, and depths measured at three points on each transect, to generate mean width and depth measures for each monitoring site. Distance to the nearest trout-free galaxiid source was calculated in the same way as the riverscape surveys.

Data analyses

I evaluated the effect of configuration of sources on *G. vulgaris* distributions in three steps. Firstly I tested whether *G. vulgaris* biomass decreased with distance to demographic sources at quantitative sites, which could indicate restriction of adult galaxiid immigration into more distant sink sites. Secondly, I tested whether distance to source could predict overall distributions of *G. vulgaris* across the trout-invaded riverscape using the extensive survey occurrence data. Thirdly, I evaluated the presence of a distance-to-source effect mediated by local habitat conditions, using a combination of non-parametric statistical approaches. I also assessed the role of habitat in restricting the distribution of large trout across the riverscape.

The effect of distance to the nearest trout-barrier on seasonal biomass of *G. vulgaris* at monitoring sites was tested using general linear models with seasons as repeated measures. I separately assessed sink and pseudosink sites, as only sink populations would be wholly dependent on immigration from sources to persist in the riverscape (Pulliam 1996). To assess potential drivers of *G. vulgaris* distributions in the riverscape dataset, I tested the effect of habitat, trout presence and distance to nearby sources on *G. vulgaris* presence. I used logistic regression to parametrically assess *G. vulgaris* presence-absence patterns (Quinn and Keough 2002). Since *G. vulgaris* was detected at very few sites in the trout-invaded riverscape during winter compared to summer, I confined my analyses to the summer dataset.

Next I searched for interactive effects of habitat conditions and demographic source proximity on *G. vulgaris* distributions. Absences of *G. vulgaris* far from sources at one end of a habitat gradient were interpreted as limit responses in the pattern of galaxiid occurrences along that gradient. Limit responses refer to the upper or lower limits of data spread in organism responses to environmental gradients, which can reveal more about the bounding environmental factors controlling organisms than central responses to individual factors that may be blurred by other unmeasured factors (Lancaster and Belyea 2006). A detectable limit response would indicate an interaction between propagule pressure and habitat conditions affecting co-occurrence with trout. I chose to search for limit responses because they would indicate overall restriction of *G. vulgaris*' occurrence away from sources, whereas presences and

absences within the limit could be driven by multiple unmeasured factors that were not related to propagule pressure.

I used a Non Parametric Screening Procedure (NPSP) to detect probable upper and lower limit responses in associations between distance to source and various habitat metrics (Konrad et al. 2008). This automated procedure calculates the probability of a low number of data points being found in a quadrant of an XY plot, thereby detecting positive or negative upper (ceiling) or lower (floor) limit responses. Habitat variables that revealed a significant positive or negative ceiling in the subset of sites containing *G. vulgaris*, but no significant ceiling in the overall dataset, were taken to represent possible exclusion of galaxiids along that habitat gradient.

Limit responses were further evaluated with quantile regression, which calculates a linear function defining the upper or lower limits for a set proportion of a dependent variable's response to an independent variable (Cade and Noon 2003). This technique can therefore illustrate the upper limits of population and community responses to habitat gradients (Konrad et al. 2008). The 90^{th} quantile was fitted so the analysis would be robust to outliers, which could disproportionately affect the slope of the function. I assessed the rigour of the plotted 90^{th} quantile slope by using bootstrapped standard errors of its coefficient to test whether it differed significantly from zero.

Finally I examined the ability of habitat factors to predict large trout occurrence in the riverscape using logistic regression. I also explicitly examined the relationship between large trout densities at quantitative monitoring sites and riverbed disturbance, as well as their seasonal occurrence across the disturbance gradient. Fish biomass data were square root transformed for parametric correlations and modelling analyses, while habitat data were $\log_e$ or arcsin-square-root transformed to meet assumptions of normality and homoscedasticity of variances. All parametric analyses were performed using Statistica 8 (Statsoft 2007), while quantile regressions were generated and tested for significance using the quantreg package in R (R Development Core Team 2007). The NPSP macro of Konrad et al. (2008) was run in Microsoft Excel.

RESULTS

General fish occurrence patterns

Galaxias vulgaris occurred at four out of eight quantitative sink sites and three out of four pseudosink sites in winter. They occurred at five sink sites and all-four pseudosink sites in summer. *Galaxias vulgaris* were also recorded at 18 out of 80 riverscape survey sites in summer. Large trout were only recorded at one sink site in winter, while in summer they occurred at six sink sites and three pseudosink sites. Winter riverscape surveys detected large trout at ten sites while winter surveys detected them at eight sites.

Influence of riverscape configuration on *G. vulgaris* distributions

A significant negative effect of distance to barrier on seasonal *G. vulgaris* biomass was detected at sink sites by a repeated measures linear model (Table 1, Figure 3). *Galaxias vulgaris* biomass was high but variable close to barriers, while *G. vulgaris* were absent from most sites further than 800 m from putative sources of dispersing immigrants (Figure 3).

Table 1: Repeated measures general linear models testing interactions between distance-to-barrier and seasonal fluctuation (repeated measure: summer vs. winter) of *G. vulgaris* biomass at putative sink and pseudosink sites. Significant effects in bold.

Effect	df	F	p
Sink sites			
distance	**1**	**17.355**	**0.006**
season	1	1.365	0.287
distance x season	1	1.299	0.298
error	6		
Pseudosink sites			
distance	1	0.010	0.929
season	1	0.168	0.722
distance x season	1	0.000	0.994
error	2		

No significant effects of distance or season were found at pseudosink sites (Table 1), though low statistical power from the number of sites may have contributed to the null result. No significant association between *G. vulgaris* occurrence and distance to source (parameter estimate = 0.43, p = 0.20), or any other habitat variable (all parameters, p > 0.14), were revealed by logistic regression modelling of *G. vulgaris* riverscape distributions.

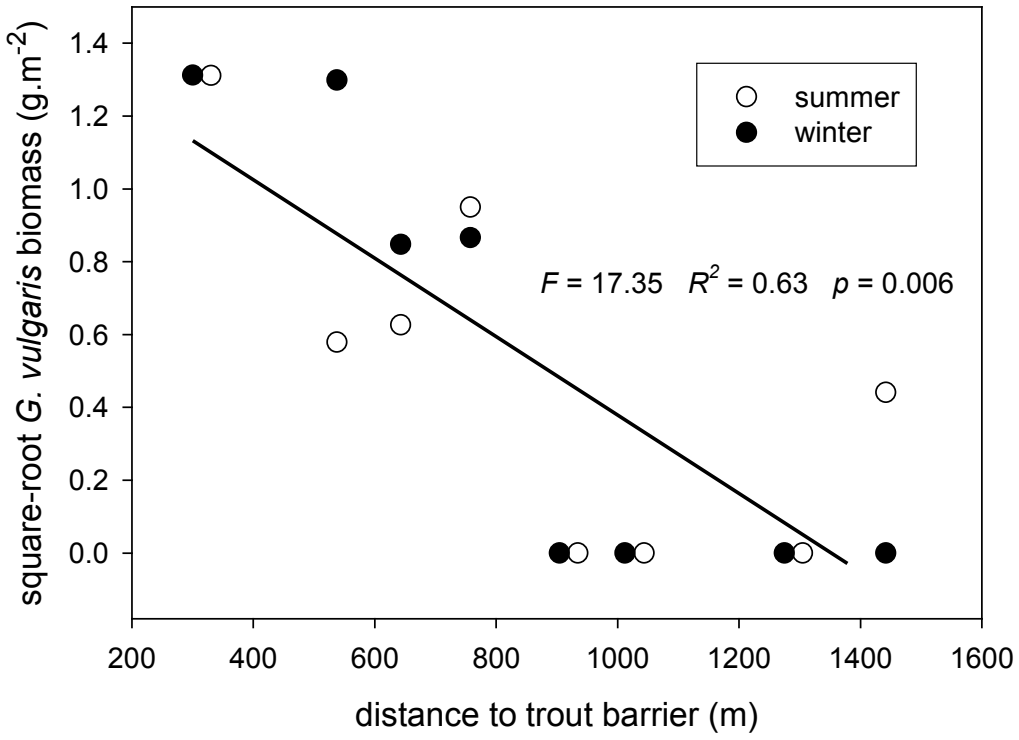

Figure 3: Change in seasonal biomass of *G. vulgaris* at sink sites with increasing distance to the nearest trout barrier. Regression line represents a significant linear response as calculated by the repeated measures general linear model. Summer sites with zero biomass are offset by 30 m to avoid overlap with winter sites.

A significant positive limit response (p < 0.05) in the distance *G. vulgaris* occurred from sources was detected along the stream width gradient by NPSP analysis. No significant ceilings existed for any habitat variable in the overall dataset (p > 0.05). Ninetieth quantile regression indicated a positive limit response of distance to barrier with increasing stream width (slope = 352.34, se = 135.73, t = 2.59, p = 0.02). This

result indicates *Galaxias vulgaris* were excluded from small reaches far from sources, but not from large reaches. A significant floor (positive lower limit, $p < 0.05$) was also identified for the distance-stream width relationship, but this was due to a lack of wide sampling sites close to trout barriers (Figure 4a). Stream size and disturbance were correlated across the riverscape (Table 2).

Although a positive ceiling was not detected by the NPSP for *G. vulgaris* occurrence and disturbance ($p > 0.05$), visual assessment of the relationship revealed a similar region of potential exclusion at distal sites with low disturbance (Figure 4b). Furthermore the 90th quantile of *G. vulgaris* distributions indicated a positive limit response of distance-to-barrier with increasing disturbance (slope = 55.48, se = 10.21, $t = 5.43$, $p < 0.0001$; Figure 4b). While "sink" monitoring sites occurred both above and below the fitted limit response, "pseudosink" sites were generally located below the limit (Figure 4).

Table 2: Significant ($p < 0.05$) Pearson's correlations (R) for stream depth, width, disturbance and percentage of overhanging vegetative bank cover at all sampling sites.

	depth	width	disturbance	% bank cover
Quantitative monitoring sites				
depth		0.75		-0.67
width	0.75			
disturbance				-0.86
% bank cover		-0.67	-0.86	
Riverscape survey sites				
depth		0.24		
width	0.24		0.42	-0.58
disturbance		0.42		-0.42
% bank cover		-0.58	-0.42	

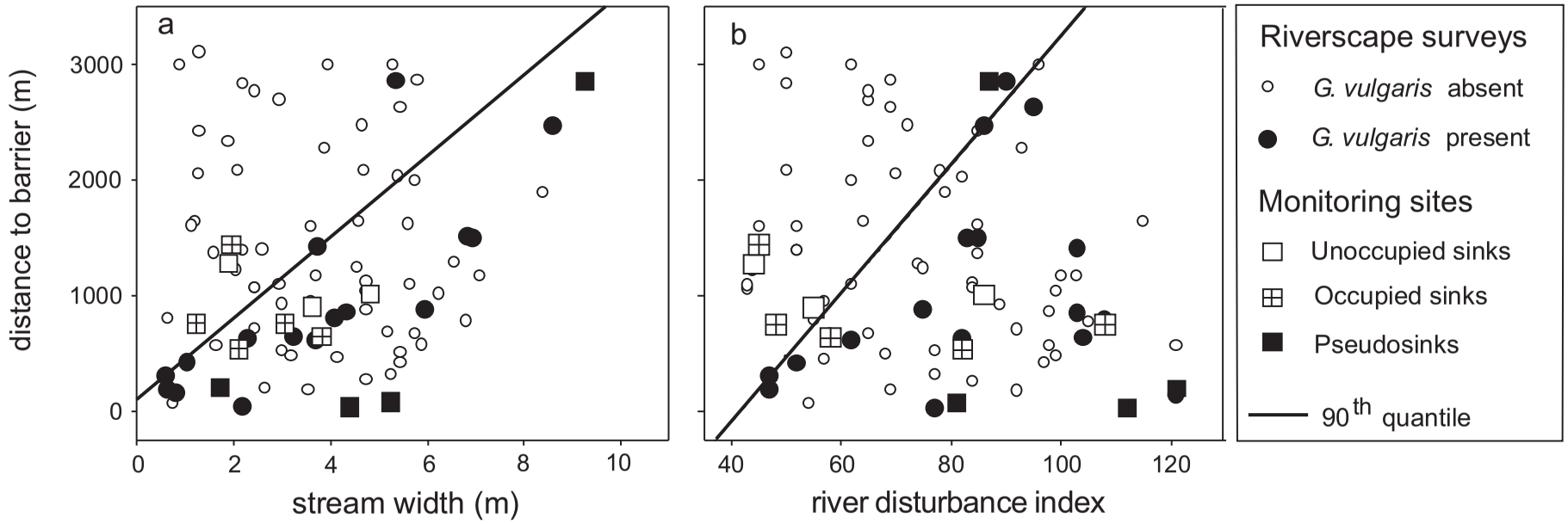

Figure 4: Putative limit responses of *G. vulgaris* occurrence at varying distances from the nearest trout barrier (illustrated by 90th quantile regression) when plotted on gradients of stream width (a) and stream disturbance (b). Spot fishing presences and absences are represented by circles, while quantitatively sampled monitoring sites are represented by squares.

Large trout habitat interactions

Logistic regression modelling indicated large trout were consistently found in narrower and deeper habitats in both seasons, and were negatively associated with riverbed disturbance in winter but not in summer (Table 3). The seasonal variation occurred because they were restricted to stable reaches in winter, but found across the riverscape in summer (Figure 5a). Moreover, biomass of large trout at quantitative sites in summer was also negatively correlated with disturbance ($r = -0.61$, $p = 0.03$; Figure 5b), as well as width ($r = -0.58$, $p = 0.04$). Large trout were therefore restricted to stable streams in the winter, and while their range appeared to expand into more disturbed reaches in the summer, per unit area biomass remained highest in small, stable streams.

Table 3: Habitat predictors of large (>150 mm FL) trout presence within trout-invaded stream reaches in winter and summer based on a logistic regression model. Significant habitat associations are in bold.

Variable	Estimate	Wald Statistic	p
Winter			
depth	2.61	3.81	0.05
width	-1.14	1.62	0.20
disturbance	**-5.75**	**5.62**	**0.02**
emergent vegetation	-3.92	2.28	0.13
submerged vegetation	4.03	2.60	0.11
overhanging vegetation	-2.37	0.03	0.85
Summer			
depth	**6.64**	**12.19**	**>0.001**
width	**-3.82**	**8.33**	**0.004**
disturbance	1.22	0.44	0.51
emergent vegetation	-1.34	0.83	0.35
submerged vegetation	2.25	1.64	0.19
overhanging vegetation	1.36	1.39	0.23

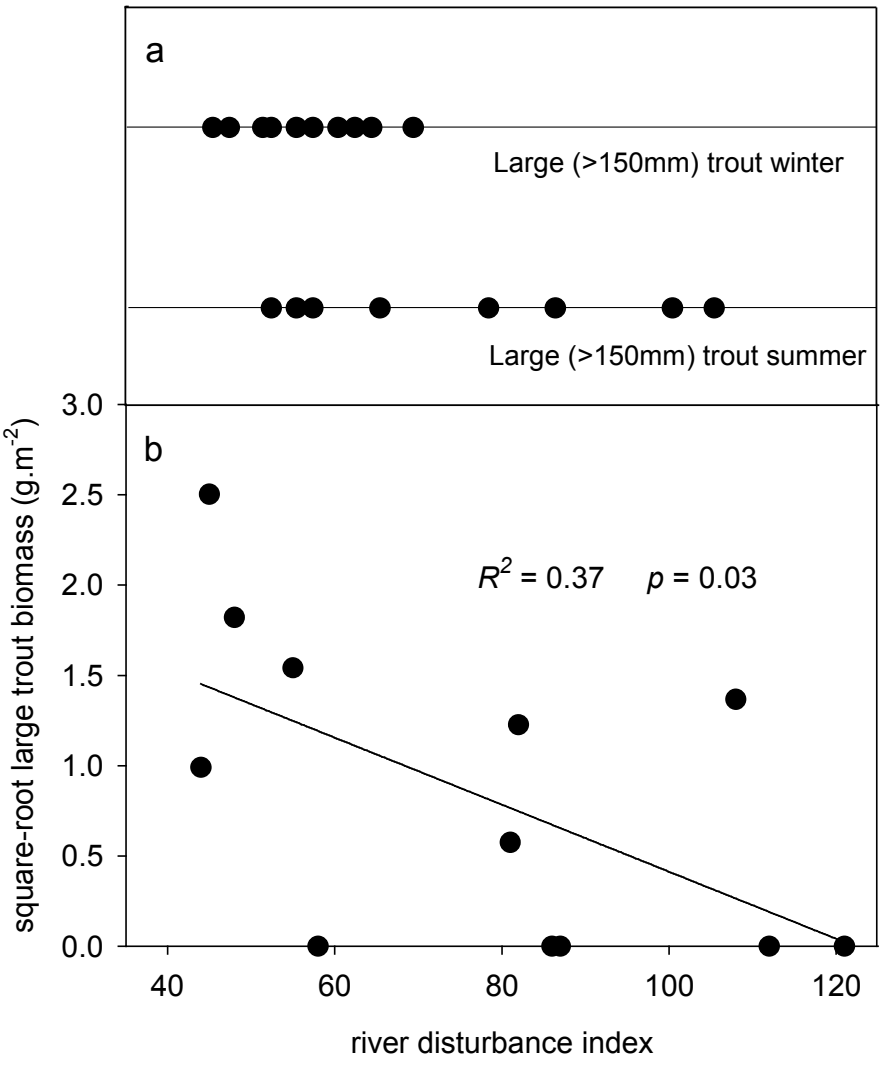

Figure 5: Habitat occupancy (a) by large (>150 mm FL) trout across the flood disturbance gradient in winter (2006) and summer (2007) riverscape surveys, and the relationship between disturbance and large trout biomass (b) recorded at quantitative monitoring sites in summer 2007. Flood disturbance was measured using a river disturbance index (Pfankuch 1975), which evaluates riverbed disturbance linked to flow variability.

DISCUSSION

This study provides evidence of an interactive effect of distance from demographic sources and local habitat in excluding *G. vulgaris* from parts of a river network containing an introduced predator. The results highlight the importance of habitat configuration in controlling predator-prey interactions at a landscape scale, and the value of multi-scale sampling for detecting these interactions.

Drivers of *G. vulgaris* distributions within sink habitat

The spatial arrangement of source and sink patches across landscapes can drive population viability within those patches (Foppen et al. 2000, With and King 2001, Nol et al. 2005). Decreases in sink patch occupancy by forest birds have been explicitly linked to increasing distances to sources (Nol et al. 2005). The significant decline in *G. vulgaris* biomass with increasing distance from sources strongly suggests propagule pressure from sources is an important factor in maintaining populations when local recruitment is negligible. Extensive, long-term monitoring of individual fish would be needed to empirically demonstrate dispersal patterns *G. vulgaris*, which was not feasible given this study's spatial scale and the logistical challenges of collecting such data (Cadwallader 1976a, Dunn 2003, Homel and Budy 2008). Nonetheless, available information on *G. vulgaris* demography and behaviour offer strong inferential support for maintenance of sink populations through dispersal. The lack of young-of-year *G. vulgaris* at sink sites suggests immigration by adults from trout-free sources is the primary mechanism promoting local population persistence (Chapter 2). Moreover adult *G. vulgaris* rapidly re-colonise habitat left vacant by drying disturbance, and the speed of colonisation is dependent on distance to wetted refugia (Davey and Kelly 2007). Habitat-seeking dispersal of *G. vulgaris* from trout-free refugia to trout-invaded sinks can therefore explain the patterns of habitat occupancy at sink sites.

In contrast to the monitoring sites, overall *G. vulgaris* occurrence in the riverscape survey was not predicted by distance to source or any other habitat characteristics. The location of *G. vulgaris* in the riverscape relative to trout barriers was, however, significantly linked to stream size and, by association, with disturbance. *Galaxias vulgaris* were excluded from distal reaches that were either small or stable, and a

positive limit response in distance-to-barrier existed along both habitat gradients. The apparent interaction between habitat, predation pressure and propagule pressure made detecting the effect of distance-to-barrier difficult with logistic regression. By searching for limit responses in *G. vulgaris* distributions, I was able to detect the limiting effect of distance to sources, even though interactions with multiple habitat factors appeared to obscure its individual effect on galaxiid occurrence. Researchers should consider whether the overall limit of a species' response to its environment is more meaningful to assess than its central responses to multiple, potentially interacting factors (Lancaster and Belyea 2006).

A likely driver of the exclusion patterns detected in *G. vulgaris* was the distribution of large predatory trout across the riverscape. Stable streams contained large trout in both winter and summer, while more disturbed reaches only contained them in summer, a period of stable flows across the riverscape. Furthermore, large trout occurrence was positively associated with narrow reaches in summer, while they retained their highest summer densities in narrow, stable monitoring sites. Thus, seasonal flooding appears to have restricted most large trout to small, stable tributaries. Densities and distributions of both species of trout recorded in the riverscapes (*O. mykiss* and *S. trutta*) are negatively affected by flooding in other New Zealand streams (Jowett and Richardson 1989, Jowett 1990). Disturbance-sensitive introduced predators can eliminate native prey in habitat patches with low levels of natural disturbance, as they are able to maintain sufficient population densities in those patches across seasons (Maret et al. 2006). The apparent seasonal expansion and contraction of large trout distributions in this study demonstrates that while predators and prey may encounter each other throughout the landscape, it is in patches displaying consistent, high density predator occupancy where the native prey are most at risk.

Galaxias vulgaris is likely to suffer high mortality in small, stable streams that provide permanent habitat for large predatory trout, and only sites close enough to potential sources of adult immigrants appeared able to sustain persistent local populations of *G. vulgaris*. Low habitat heterogeneity and high predator densities can both maximise predator-prey encounter rates (Beukers and Jones 1998, Crook and Robertson 1999). Consequently a synergistic effect involving stream narrowness and

low disturbance that promotes exclusion of *G. vulgaris* by trout from these reaches is likely. While some spring-fed tributaries contained submerged macrophytes that appeared to enhance co-occurrence between trout and another galaxiid species (Chapter 3), there was no evidence that vegetative cover enabled persistence of *G. vulgaris* in sink reaches far from sources.

In contrast, very large or highly disturbed sites contained *G. vulgaris* up to three kilometres away from the nearest source. These sites seldom contained large trout, but added habitat complexity in the form of variable stream profiles and channel braiding may also enhance the ability of *G. vulgaris* to persist within them. Non-diadromous galaxiids are known to avoid interacting with trout through microhabitat separation (Glova and Sagar 1993; McIntosh et al. 1992). These mechanisms would promote prolonged persistence of *G. vulgaris* despite little immigration from sources, although a small proportion of distant occupied sites (including one monitoring site) were likely pseudosink habitats (i.e. habitat where sporadic positive population growth was possible). Juvenile recruitment of *G. vulgaris* occurred at these sites, presumably due to release from high predation pressure by trout (Chapter 2). Such local recruitment would allow persistence independent of immigration, despite having a low carrying capacity (Pulliam 1996). Nevertheless, the general rarity of pseudosink habitat across the riverscape in general (Chapter 2), suggests overall *G. vulgaris* occurrence patterns were dependent on propagule pressure from sources. It is likely that in river networks where flow-related disturbance was more widespread, pseudosink habitat could play a larger role in driving galaxiid occurrence.

Assessing the spatial context of invasive predator impacts

Fish interact with their environment at many different scales (Schlosser 1991, Schlosser 1995), so multiple-scale sampling and continuously assessing species distributions across riverscapes offers good prospects for better assessing these interactions, even though the logistics of such approaches can be challenging (Fausch et al. 2002, Le Pichon et al. 2006). Use of electrofishing made continuous surveys impractical in this study, but the combination of extensive low-intensity sampling across the riverscape with selective high-intensity sampling at the reach scale enabled detection of spatially-explicit interactions between *G. vulgaris* and its predator. This approach offers a potential compromise between extensive and intensive measures of

fish distributions, although the ability of the spot-fishing technique to detect some species better than others means the biology of the target species should be carefully considered when choosing a sampling methodology.

The spatial structuring of predator-prey co-occurrence in this study offers new insights into invasive predator effects across landscapes. My data indicate the location of predator-free sources can directly affect population persistence within invaded habitat, and this effect is likely mediated by habitat controlling predation pressure. While spatially explicit analysis of distributions is crucial for understanding species-habitat interactions (Schlosser 1995, Wiegand et al. 1999, With and King 2001), my findings suggest assessing spatial configuration of ecosystems will also improve the interpretation of interspecific interactions. Invasive predator impacts in streams can be minimised by habitat complexity or natural disturbance (Meffe 1984, Baber et al. 2004, Leprieur et al. 2006). Understanding how these abiotic factors shift across riverscapes and landscapes will allow scientists and managers to better predict the spatial variability of invasive predator impacts and target management activities appropriately.

Conservation implications

Galaxias vulgaris, while clearly threatened by trout, is currently not included in a government recovery plan aimed at protection New Zealand's threatened non-diadromous galaxiid fish (Department of Conservation 2004). This is likely a result of the apparent regularity with which the species co-occurs with trout (Chapter 2), which contrasts sharply with the strict species-complementarity often seen for other non-diadromous galaxiids in other, more stable trout-invaded basins in New Zealand (e.g., Townsend 1996). It is possible that those systems, by being more hydrologically stable and geomorphologically uniform than the larger reaches in this study, enable trout to exert greater predation pressure on non-migratory galaxiids. For example, Townsend and Crowl (1991) found non-migratory galaxiids at only 9 out of 78 trout-occupied sites in tributaries of the Taieri catchment, and all these co-occurrence sites had braided, unstable river channels. The configuration and prevalence of hydrologically disturbed reaches within the Taieri River network could have played a significant role in the decline of these species following tout invasion, and their

differing susceptibility to trout predation relative to *G. vulgaris* may be more a function of contrasting riverscapes than differences in anti-predator adaptations.

The spatial patterns documented here indicate adding or expanding source reaches to a source-sink riverscape would likely enhance overall population persistence, by decreasing dispersal distances between sources and sinks. Increasing source areas in terrestrial ecosystem can enhance occupancy of sink habitats (Nol et al. 2005), and thus local rehabilitation efforts in sources could have consequences at larger spatial scales. The configuration of dispersal pathways can have a critical effect on source-sink dynamics in river networks (Schick and Lindley 2007), and although the ability of habitat to support translocated species is an important selection criterion for choosing streams for rehabilitation (Harig and Fausch 2002), its position within the river network may be as important for maximising conservation gains. For example, a rehabilitated stream close to an extant source population in the network may not have as much of an effect on predator-prey coexistence across the riverscape than one in a tributary far from other sources.

A drawback of creating refugia for native fish by separating them from invaders by barriers is that these barriers can make the refuge populations susceptible to stochastic extinction through isolation (Dunham and Rieman 1999, Fausch et al. 2009). To successfully create source streams for threatened species in invader-driven sink riverscapes, any barriers used or created to protect the native fish from invasion must allow the native species to disperse across them. A correctly designed barrier will enhance the persistence of the newly created population, while at the same time ensuring it contributes to sustained occupancy of nearby predator dominated sink reaches.

ACKNOWLEDGMENTS

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Plate 4: A waterfall protects *Galaxias vulgaris* from trout in the Otamatapaio River, Waitaki Basin.

Chapter 5

Development of a spatial model predicting exclusion of a vulnerable native fish by introduced trout based on landscape features

ABSRACT

Habitat variability can affect the ability of invasive predators to exclude native prey species from parts of a landscape. If habitat consistently mediates predator impacts, the outcome of predator-prey interactions could be modelled using habitat data alone. In New Zealand streams, invasive predatory trout create source-sink dynamics in populations of the native fish *Galaxias vulgaris*. Within trout-invaded sink habitat, *G. vulgaris* are excluded from small, stable streams that occur far from galaxiid demographic sources (streams above barriers to trout). I developed a GIS-based spatial model to predict where trout would exclude *G. vulgaris* in a river network, based on stream size and distance-to-source. The maximum distance from source streams at which *G. vulgaris* could co-occur with trout was modelled in two trout-invaded riverscapes using a quantile limit function in ArcGIS. I tested the predictive ability of the model using training datasets and data from two other catchments where fish occurrence patterns were quantified from electrofishing surveys. The model correctly predicted *G. vulgaris* absence in the first test catchment, but failed to predict absence in the second test dataset. Successful model validation was dependent on knowledge of all demographic sources and access to sufficient survey data. The model demonstrated the ability to predict *G. vulgaris* exclusion by trout, highlighting the importance of habitat configuration in driving interspecific interactions at a landscape scale. The current model could be used detect undiscovered trout-free source populations, which are important targets for galaxiid conservation efforts, and could also aid in selecting streams for rehabilitation through trout eradication. Since species interaction models based on landscape data are likely to be generally useful in guiding conservation management, researchers should investigate whether other biotic interactions that can be consistently predicted by habitat exist in nature.

INTRODUCTION

Biotic invasions negatively impact native species populations (Vitousek et al. 1996, Ricciardi 2007), and much effort has been dedicated to modelling and predicting the spread and impacts of invasive species (Karieva 1996, Moyle and Light 1996b, Shea and Chesson 2002, Park 2004). While it is clear that the environment plays a key role in enabling or preventing the spread of invaders (Shea and Chesson 2002, White et al. 2008), knowledge of how the environment mediates their impacts on native species is still poor (Brook 2008, Ruiz et al. 1999). There is an increasing need to develop models that can predict how the environment affects outcomes of native-invasive species interactions, particularly as this knowledge is crucial to invasive species management strategies (Hulme 2006).

The need for such predictive models is especially urgent in freshwater ecosystems, which are disproportionately affected by introduced predators (Cox and Lima 2006). Introduced predatory salmonid fishes (trout and chars), in particular, have altered aquatic communities and ecosystems at multiple spatial scales (Pilliod and Peterson 2001, Townsend 2003, Finlay and Vredenburg 2007). Habitat variability can affect the success of fish invasions across landscapes (Gido and Brown 1999, Fausch et al. 2001), but once they do establish their impact on native species may also vary spatially (Labbe and Fausch 2000). For example, the negative pressure exerted by introduced predatory fish on native species can be mediated by high flow variability (Meffe 1984, Closs and Lake 1996, Leprieur et al. 2006), or by local habitat heterogeneity (Baber et al. 2004, Stuart-Smith et al. 2007).

For a model to predict such interactions, it must be applicable at a scale that captures the extent of the invasive species distribution, but have a fine enough resolution to encompass the influence of local habitat features on the interactions. By using a scale intermediate between entire catchments and the local reach scale where fish-habitat interactions occur, the interaction between fish and their habitat across a "riverscape" can be most effectively modelled (Fausch et al. 2002). Fish distributions are, however, particularly difficult to continuously map using conventional sampling methods (Duncan and Kubecka 1996), making this a challenging scale to work at. Nevertheless, because landscape-scale habitat patterns may have a direct effect on the

local impact of the invader (Labbe and Fausch 2000, Leprieur et al. 2006), it may be more practical to search for abiotic drivers of invader-impact severity and to model these drivers across landscapes as a proxy for invader impacts. This approach offers the potential for managers to use available geographic information as input data, rather than depending on costly and time-consuming surveys of invader distributions. The increasing availability of detailed remote-sensed habitat information further reduces the amount of fieldwork required to acquire adequate habitat data (Kerr and Ostrovsky 2003), making desktop analyses possible.

Such an approach may be particularly useful in the river networks of New Zealand, where introduced trout threaten native fishes. The country contains a highly endemic freshwater fish fauna, including several species of non-diadromous galaxiid fishes threatened by non-native brown (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum) introduced for sport fishing (McDowall 2000, McDowall 2006). Several galaxiid species have distributions that do not overlap with trout, suggesting previous extirpation by the introduced predator (Townsend 1996, McDowall 2006). However, one species, the Canterbury galaxias (*Galaxias vulgaris* Stokell), co-occurs regularly with trout (Glova et al. 1992, McIntosh 2000, Davey and Kelly 2007). *Galaxias vulgaris* forms source-sink metapopulations in trout-invaded river networks, with trout-free refuge streams acting as demographic sources of colonists for sink streams (Chapter 2). In Waimakariri River tributaries, dispersal distance from trout-free source streams interacts with habitat patterns to mediate co-occurrence between *G. vulgaris* and trout. *Galaxias vulgaris* were excluded by trout from small, stable streams far from sources, where predation pressure by large trout was severe (Chapter 4).

The exclusion of *G. vulgaris* from small, distal stream reaches represents a linear limit response (*sensu* Lancaster and Belyea 2006) in the distance *G. vulgaris* can occur from demographic sources in relation to stream size. Such relationships can be modelled with quantile regression, where a linear function is fit to the upper limit of the dependent variable's response to an independent variable (Cade and Noon 2003). In this study I used such a function to construct a simple spatial model predicting exclusion of *G. vulgaris* by trout, using digitised geographic data for local stream size and distance to the nearest source of *G. vulgaris* recruitment. I tested if I could predict

reaches where trout eliminated *G. vulgaris* by applying the galaxiid exclusion model across riverscapes where *G. vulgaris* and trout co-occurred. I also assessed applicability of the model as a management tool for conserving *G. vulgaris*, by indicating potential localities of unknown sources, and prioritising streams for active management. The model was constructed in a Geographical Information System (GIS), and its predictive ability was tested both within the catchments where the pattern was discovered and in other spatially distant catchments containing trout and *G. vulgaris*.

METHODS

Collection of model training data

Electrofishing data from two sub-catchments of the upper Waimakariri River, where the exclusion phenomenon was originally detected were used as training data for the GIS model (Figure 1). The sub-catchments (riverscapes), which drain the eastern slopes of the Southern Alps, South Island, New Zealand, included four tributaries of upper Broken River and three tributaries of upper Porter River These were habitat-diverse riverscapes where both trout and galaxiids occurred (McIntosh 2000, Jellyman and McIntosh 2008). Surveys were conducted on both riverscapes in summer (February 2007), with a follow-up survey in March 2008 to expand the range of habitat variability sampled.

Electrofishing surveys were conducted at 80 reaches, spread across the Porter and Broken River networks. Three areas, approximately one meter by two meters, were electrofished within each reach. Electrofishing, using a Kainga EFM 300 backpack electrofisher (NIWA instrument Systems, N.Z.) generating 400-600V pulsed DC current, was conducted downstream into a push net. Downstream fishing into a pushnet is standard practice for catching benthic galaxiids in New Zealand streams (Townsend and Crowl 1991). Validation of the sub-sampling approach showed a 72% detection rate for *G. vulgaris* in the training catchments, with false absences being recorded where *G. vulgaris* were present at extremely low densities (<0.03 fish/m^2; Chapter 4). All captured fish were identified to species before being returned to the survey reach. The location of each survey reach was recorded using a Trimble©

GEO-XM hand-held geographic positioning system, and waypoint data were differentially corrected to a horizontal accuracy of two to ten metres.

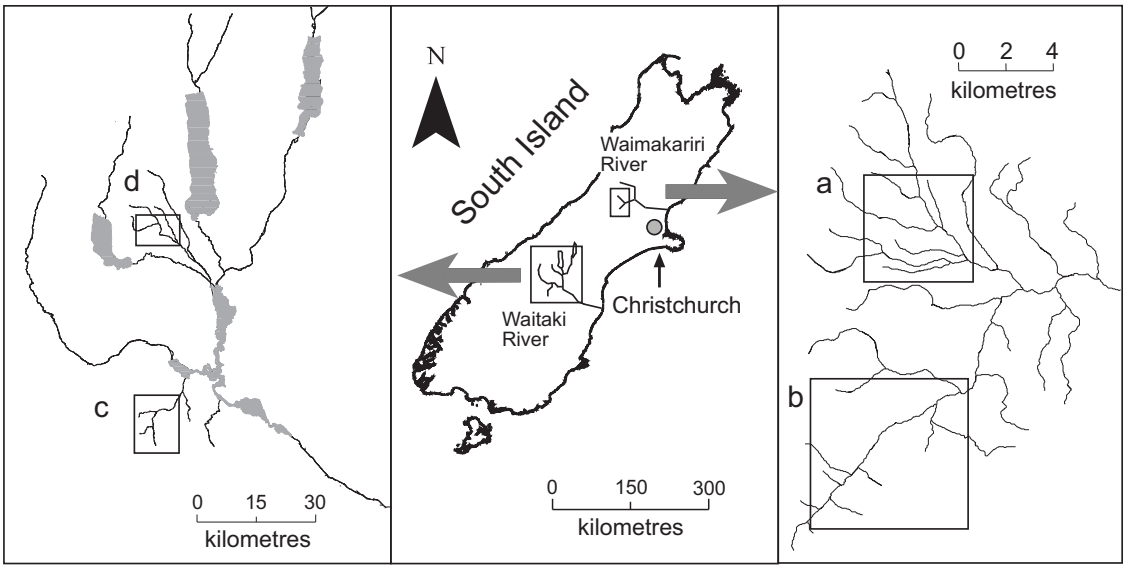

Figure 1: Location of model training and testing river networks in the Waimakariri and Waitaki Rivers, South Island, New Zealand. Training river networks included a) Porter River and b) Broken River (shown in detail in Figure 3), and testing river networks included the c) Otamatapaio (Figure 4) and d) Fraser rivers (Figure 5).

Collection of model testing data

Results from a survey conducted in September 2006 (austral winter) across the Broken and Porter riverscapes using the same protocols was used as an independent test dataset. Surveys were also conducted in two other riverscapes within the upper Waitaki River basin, which also flows east from the Southern Alps (Figure 1). The river system has a comparable geology and river morphology to the Waimakariri catchment, as both are located in the high country ecoregion and share similar climate and fluvial geomorphology (Harding and Winterbourn 1997). The riverscapes are characterised by streams with highly mobile greywacke sandstone gravel beds (Soons 1977), and drain tussock and grass covered hills (Burrows 1977). The Waitaki catchment contains both species of trout, *G. vulgaris* and several other non-diadromous galaxiid species (Elkington and Charteris 2005). The Otamatapaio River in the Waitaki basin comprised 84 km of combined stream length. This made it a comparable size to the combined training catchments (78 km stream length).

Exploratory fieldwork revealed three trout-free populations of *G. vulgaris* in the upper tributaries. The other riverscape, the Fraser River, was also of comparable size (56 km stream length) but was bisected by the Pukaki Canal. This is a large hydroelectric canal under which the river and several tributaries pass via culverts, potentially disrupting connectivity within the riverscape. The main stream ran through a large culvert which appeared to restrict access to the upper reaches for large migratory trout, although trout were patchily distributed upstream. A channelised spring creek that ran through a second culvert under the canal was identified as containing the only trout-free barrier population of *G. vulgaris* in the surveyed Fraser riverscape. This riverscape presented an added challenge because accessibility was limited to a few reaches on public land or where the landowner granted access.

Preparation of GIS data

All spatial analyses were performed in ArcGIS 9.1 (ESRI 2005). To model spatial exclusion of *G. vulgaris* across riverscapes I first generated raster datasets of stream size and distance-to-nearest-source for each riverscape based on the Freshwater Environments of New Zealand (FWENZ) river network, a comprehensive vector model of the rivers of New Zealand (Leathwick et al. 2008). The model comprises multiple segments, with segment ends marked by stream confluences. Each segment contained attribute data for catchment and segment scale habitat variables. I used the SegLowFlow attribute, a 4^{th}-root transformed estimate of mean annual low flow (m^3/s) derived from several landscape-scale predictors (Pearson 1995, Leathwick et al. 2008), as a proxy variable for stream size. This method provided continuous width data for all the river networks, eliminating the need for widespread field measures of stream width. The SegLowFlow attribute was chosen as it correlated well with field measures of stream width in the training dataset ($r = 0.91$, $p < 0.001$). To model distance-to-source, I derived a 25 m resolution raster from the FWENZ shape file and converted it to points, which were then located on a network dataset based on FWENZ. The Closest Facility tool in the ArcGIS Network Analyst toolkit was used to calculate the distance between each point on the network and the nearest barrier to trout invasion. These distance data were then assigned to each point and used to generate a new 25 m resolution raster of distance-to-source that could be overlaid on the stream size raster.

Modelling spatial exclusion

To mimic the distribution limit seen in *G. vulgaris* occurrences across the stream size gradient in the training catchments, I located the field sites on the FWENZ network using GPS data and calculated distance to the nearest trout barrier for each *G. vulgaris* distribution record. These distances were plotted against the SegLowFlow variable for the local stream segment (Figure 2) and the 90th quantile function of the relationship as calculated using the quantreg package in the free statistical program R (R Development Core Team 2007):

(Equation 1) $y = 22666.93x - 22052.8$

Where: y = distance to nearest trout barrier and x = SegLowFlow

The 90th quantile was chosen as a representation of the upper limit of *G. vulgaris* distributions that was sufficiently robust to obvious outliers in the relationship. The fitted slope was significantly different from zero when tested using bootstrapped standard errors (se = 971.14, t = 23.34, $p < 0.0001$). Reaches that occurred above the 90th quantile were considered an exclusion zone, where predation by trout was predicted to prevent *G. vulgaris* occurrence (Figure 2).

A series of raster calculations were performed to create trout-induced exclusion zones for *G. vulgaris*. First Equation 1 was applied using the distance-to-barrier raster (y) and the stream size raster (x). The raster produced from the equation was subtracted from the distance-to-barrier raster, creating a raster where all cells occurring above the limit response had a value >0 and cells below the response had a value <0. Finally this raster was reclassified into exclusion or co-occurrence cells based on their positive or negative value, respectively. The raster was then converted back to vector data for better mapping, and the lengths of exclusion and co-occurrence reaches measured to assess the proportion of *G. vulgaris* exclusion habitat occurring across the surveyed riverscapes.

Model validation

The validity of the model was tested by assessing where records of *G. vulgaris* presence or absence fell across training and test riverscapes. I used three methods to evaluate model success. First, the ability of the overall model to predict *G. vulgaris*

presence and absence better than random for each dataset was tested. For this I used a contingency table based on the observed vs. expected confusion matrix of each dataset (Fielding and Bell 1997). The matrix consisted of four categories of *G. vulgaris* presence/absence, namely correctly predicted presence, correctly predicted absence, incorrectly predicted presence and incorrectly predicted absence. I tested whether the spread of *G. vulgaris* presences and absences were independent of whether they fell within predicted exclusion or co-occurrence zones (after Freeman et al. 1997), using Fisher exact tests (Zar 1999). The primary purpose of the model was to predict exclusion of *G. vulgaris* above the quantile limit rather than presence below the limit. I therefore assessed the model's negative predictive power (Fielding and Bell 1997) by testing whether the probability of *G. vulgaris* being absent from the exclusion zone was significantly different from 0.5 (i.e., random) using a binomial test of single proportions (Dalgaard 2002). The consistency of the limit function in predicting the 90^{th} quantile of *G. vulgaris* records was also assessed using a binomial test. Significant deviation from the expected proportion of 10% of all *G. vulgaris* records occurring above the limit function would represent failure to correctly predict the limit response. Fisher exact tests were performed in Statistica (Statsoft 2007), while binomial tests were run in R.

Using the model to detect unknown barriers

As I assumed co-occurrences between trout and galaxiids were dependent on immigration from a source (Chapter 4), I postulated that such co-occurrences should only be possible within a certain distance from that source. An application of the spatial model was therefore to use the limit response to calculate the distance along a river network from a site of galaxiid-trout co-occurrence to where the nearest barrier population ought to be. I applied this technique to a site in the Otamatapaio test riverscape where *G. vulgaris* occurred together with trout well inside the modelled exclusion zone. I used the stream size at the site of co-occurrence to back-calculate the maximum distance to any unknown source site, using the quantile function. The maximum network distance to a potential source was modelled in GIS using a network distance raster, so that all stream reaches that fell within the 'search radius' for barriers that could contain a trout-free source were mapped. My aim was to assess the likelihood of unknown sources being responsible for the record, and the utility of the technique as a management tool to find unknown trout-free sites.

RESULTS

Model performance based on training dataset

The training dataset passed all three statistical tests of predictive success (i.e. predicted occurrence, predicted exclusion, and 90% of occurrences within co-occurrence zone). Five percent of records from the training dataset occurred in the exclusion zone, while *G. vulgaris* absence was correctly predicted 97% of the time (Table 1). The incorrect three percent was caused by a single outlier in the distance-habitat relationship (Figure 2, Figure 3). In total exclusion reaches (i.e. where it was predicted *G. vulgaris* would not co-occur with trout) comprised 43% of the combined Porter and Broken riverscapes (Table 2).

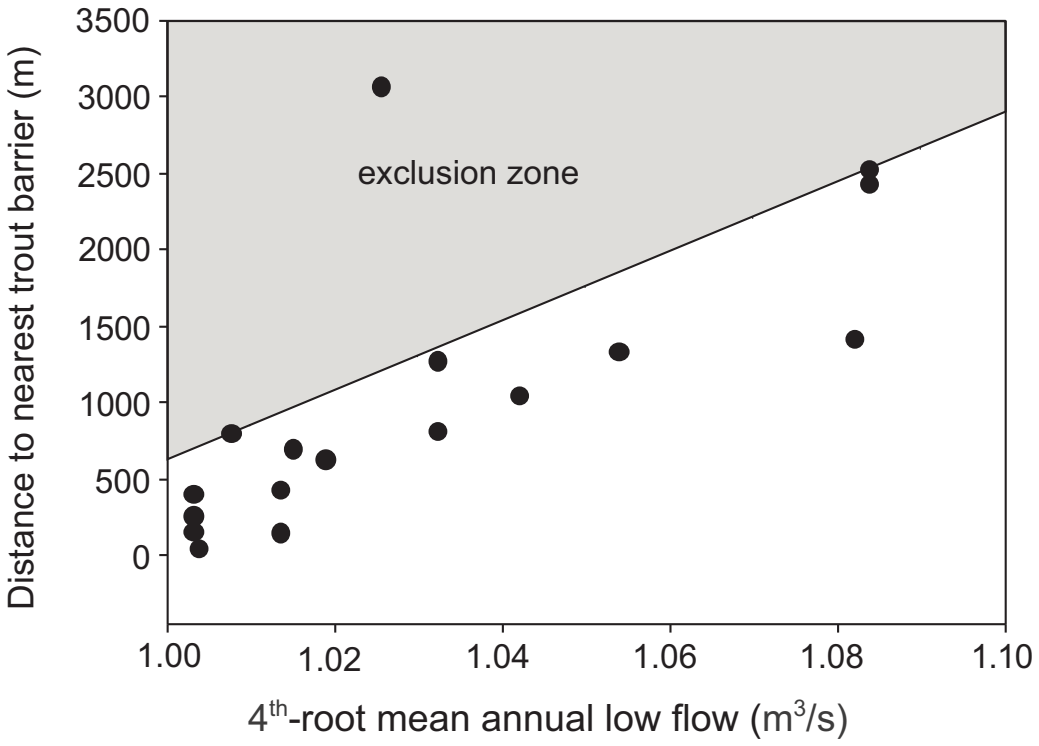

Figure 2: Ninetieth quantile regression plot of the relationship between the distance from nearest galaxiid demographic source of *G. vulgaris* occurrences (upstream of a barrier to trout movement) in the river network, and the estimated mean annual 7-day low flow at those locations. Variables were derived from the Freshwater Environments of New Zealand river network and *G. vulgaris* occurrences were obtained from electrofishing. The shaded area represents a spatial zone where trout are predicted to exclude *G. vulgaris* from the riverscape.

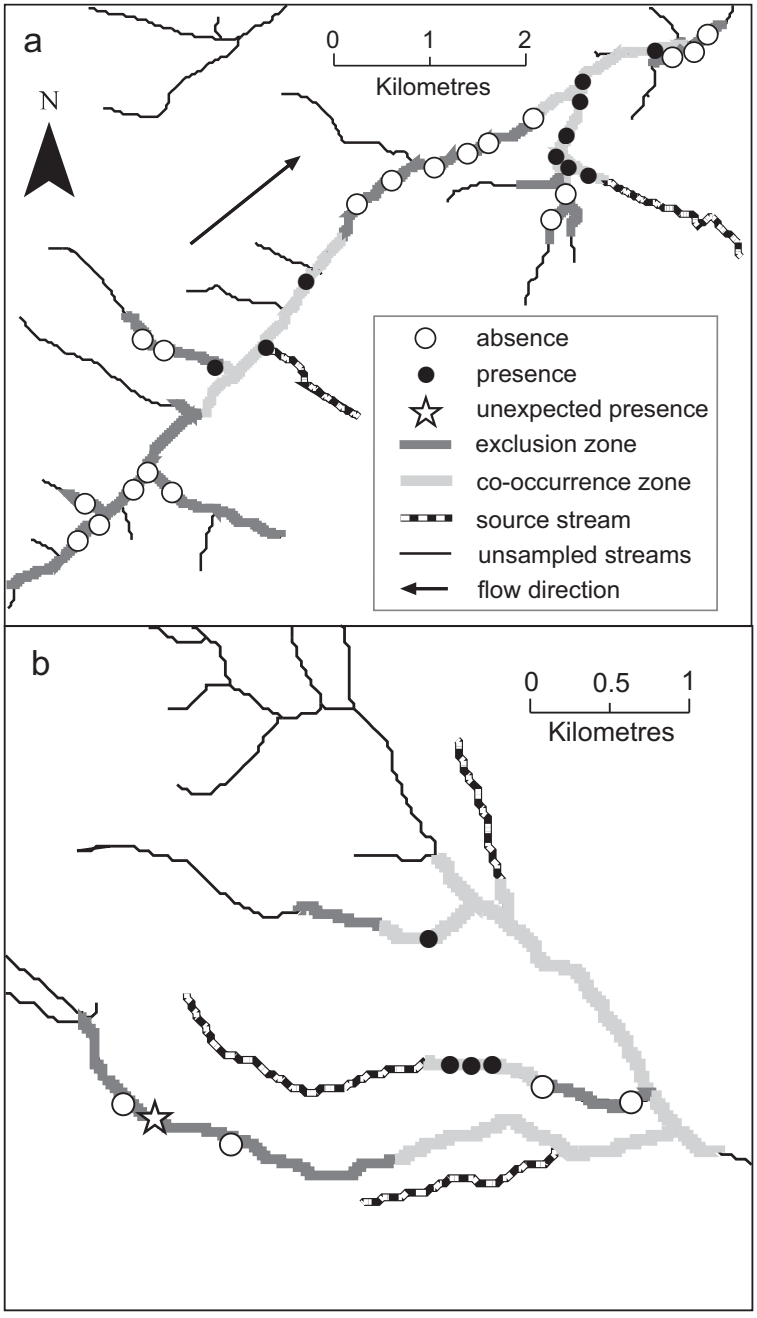

Figure 3: Spatial map of actual and predicted fish distributions in (a) the Porter River and (b) Broken River produced from the training dataset. Data from these riverscapes were combined to estimate the 90th quantile regression function, and the spatial model was subsequently applied to each riverscape and the model success rates pooled. Presences indicate detection of *G. vulgaris* by electrofishing within the modelled co-occurrence zones. Absences indicate where no *G. vulgaris* were detected within the modelled exclusion zone, while unexpected presence denotes detection of *G. vulgaris* in the exclusion zone. Source stream refers to tributaries upstream of trout barriers presumed to supply the invaded network with dispersing fish.

Table 1: Validation of a spatial model of *G. vulgaris* exclusion by trout using field records from training and multiple test datasets. Waimakariri datasets combine data from the Porter and Broken Rivers. Fraser data below canal refers to a dataset where sites upstream of a semi-permeable trout barrier were assumed to be demographic sources, so only sites downstream of the canal were modelled. Statistical results include: assessment of the proportion of correctly and incorrectly predicted *G. vulgaris* presences and absences using a Fisher exact test, a binomial test of deviation from the predicted proportion of *G. vulgaris* occurrences above the 90th quantile limit, and a binomial test for negative predictive power (NPP) in exclusion zone being significantly different from random. All result probabilities based on one degree of freedom. Significant test results are **bold**.

Dataset	Probability from Fisher exact test of overall model performance *	% All *G. vulgaris* occurrences located in exclusion zone	Probability from binomial test of 90th quantile model consistency †	Number of survey sites within exclusion zone	% Correct exclusion (NPP)	Probability from binomial test of NPP ‡
Waimakariri training data	**0.002**	5	1.0	29	97	**<0.0001**
Waimakariri test data	0.6	14	0.6	9	89	0.04
Otamatapaio test data	**<0.05**	25	0.1	23	91	**0.0001**
Fraser test data	0.6	100	**<0.0001**	33	67	0.08
Fraser data below canal	0.2	33	0.3	8	88	0.07

* H_0: Distribution of *G. vulgaris* presences random across co-occurrence and exclusion zones

† H_0: Proportion of *G. vulgaris* occurrences above limit = 0.1

‡ H_0: Proportion of sites containing *G. vulgaris* = 0.5

Model performance within training catchment

In validating the winter 2006 survey of the Porter and Broken riverscapes, the Fisher exact test indicated there was no evidence of an association between model predictions and all records of *G. vulgaris* presence and absence (Table 1, column 2). The test dataset contained only one *G. vulgaris* record within the exclusion zone, however, so that exclusion was correctly predicted at 89% of sites in this zone (Table 1, column 6). This meant the 90th quantile of *G. vulgaris* occurrences was correctly predicted for the test data, and negative predictive power was significantly better than random (Table 1, column 7).

Table 2: Relative extent of exclusion and co-occurrence zones in training and test riverscapes.

Riverscape	Percentage riverscape within co-occurrence zone	Percentage riverscape within exclusion zone
Waimakariri (Porter + Broken)	57	43
Otamatapaio	26	74
Fraser	6	94
Fraser below culverts	28	72

Model performance across test catchments

The Otamatapaio model had a high proportion of correctly predicted exclusion sites (91%) and passed all performance tests (Table 1). The Otamatapaio dataset differed from the Waimakariri dataset as the model predicted 74% of the surveyed riverscape to be an exclusion zone for *G. vulgaris* (Table 2, Figure 4).

When the entire Fraser riverscape was used in the model, it failed all three tests, and all *G. vulgaris* records occurred in the predicted exclusion zone (Table 1, Figure 5a). The model was subsequently applied only to reaches below the Pukaki Canal, with all areas upstream assumed to be demographic sources for *G. vulgaris* (Figure 5b). Under this scenario the model performed considerably better. The spread of *G. vulgaris* occurrences across exclusion and co-occurrence zones no longer deviated significantly from the 90th quantile prediction (Table 1). The dataset still failed the

other tests of model predictive success (Table 1), indicating there were still insufficient correctly predicted presences and absences relative to incorrect ones. Although there were very few survey sites left to test once the reaches above the canal had been excluded from the analysis, there was only one incorrectly predicted fish record (Figure 5b).

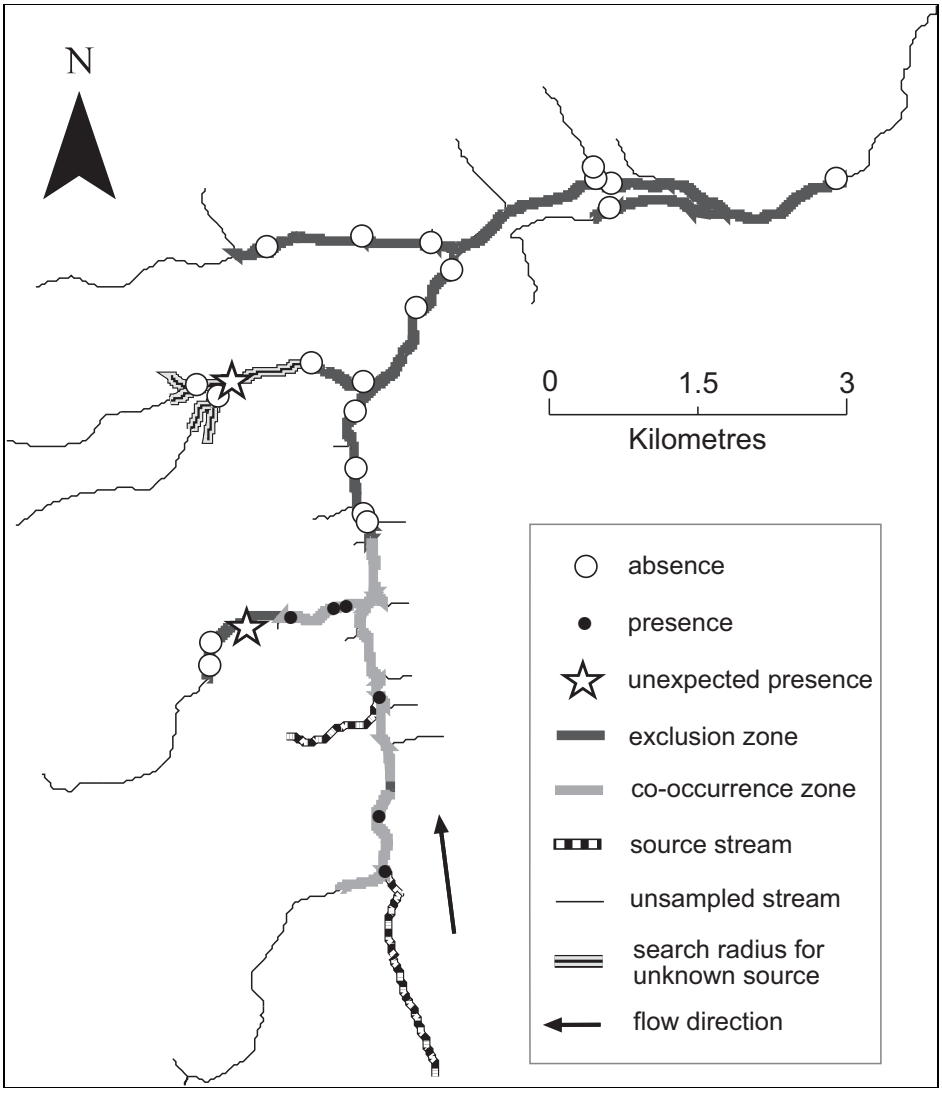

Figure 4: Spatial map of galaxiid distributions predicted by the Otamatapaio model and actual fish distribution records. The search radius for an unknown source represents the modelled maximum network distance from a *G. vulgaris* record in the exclusion zone that an unidentified source population (i.e. one above at trout limiting barrier) could be expected to occur. See Figure 3 for further explanation of symbols.

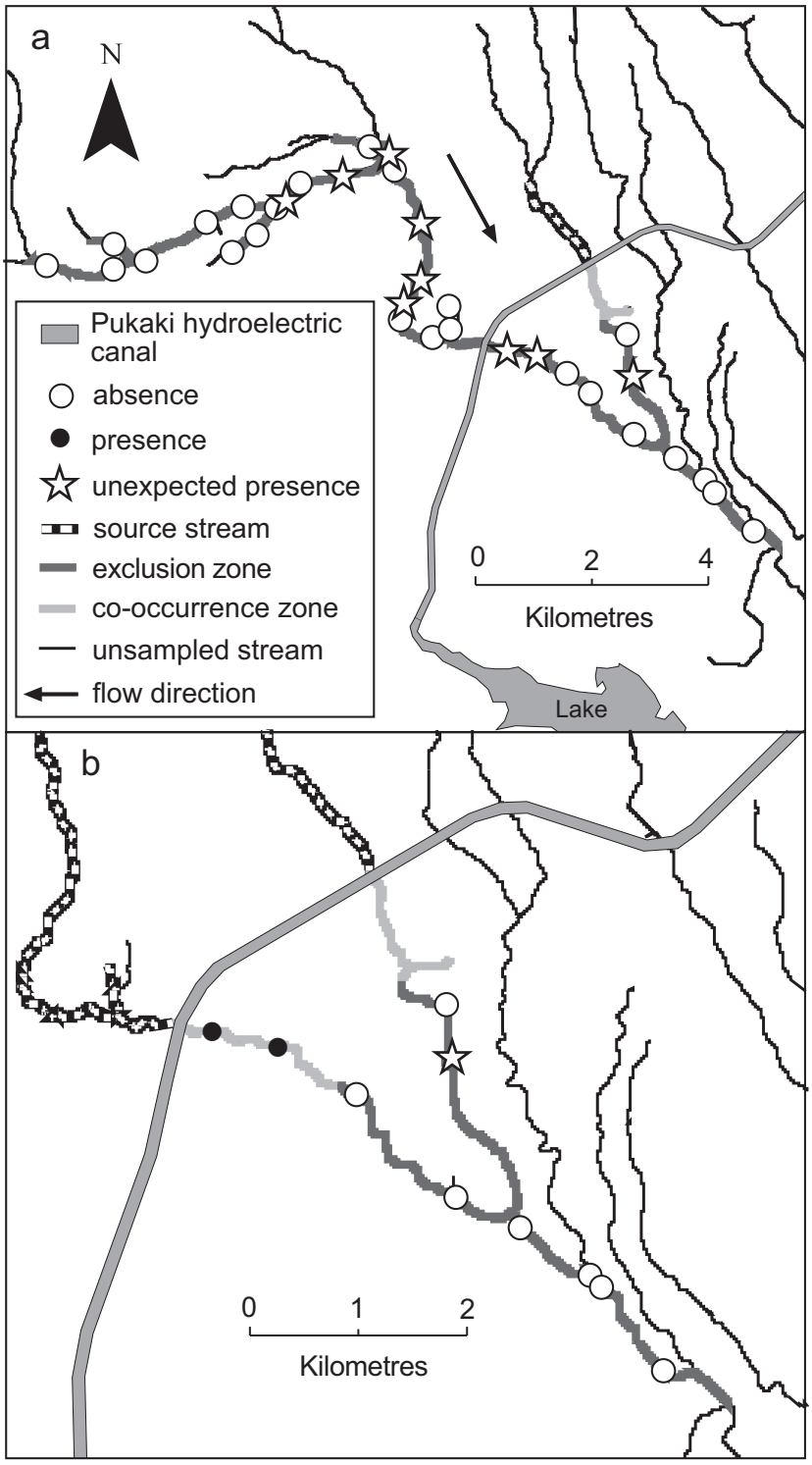

Figure 5: Spatial map of *G. vulgaris* occurrences in the Fraser River together with distributions predicted by the model when applied to (a) entire riverscape, or (b) only riverscape downstream of the Pukaki Canal, assuming all reaches upstream of the canal were demographic sources. See Figure 3 for further explanation of symbols.

Modelling distance to unknown sources

A *G. vulgaris* occurrence site in the exclusion zone of the Otamatapaio riverscape was calculated to be within 762 m of an undetected barrier using the quantile regression function (Equation 1). The modelled search radius suggests a trout-free source stream ought to occur on one of four tributaries upstream of the unexpected occurrence record (Figure 4). Pilot surveys in the lower reaches of these streams had yielded no fish, but it is possible that fish populations existed upstream of the initially sampled reaches. In a management context the model indicates more thorough exploration of these tributaries would be warranted.

DISCUSSION

GIS-based modelling of species distributions has generally focussed on understanding the environmental drivers of a species' realised niche (Hirzel and Le Lay 2008), often ignoring ecological drivers (Guisan et al. 2006). While the effect of interspecific interactions has been explored in species distribution modelling (Leathwick and Austin 2001), my study used habitat as a surrogate predictor of these interactions.

My results provide further evidence that habitat occupancy by *G. vulgaris* in trout-driven sink habitat is dependent on the landscape configuration of demographic sources. The training dataset passed all three statistical validation tests and indicated how the tests behave when assessing a perfect model result. The results of the test datasets could thus be assessed in comparison to these results. The winter dataset passed two of the three tests, including critically the test of negative predictive power. This indicates the exclusion model is transferable through time, and that there was temporal stability in the galaxiid exclusion pattern. While validation of the Fraser exclusion model was hampered first by the effect of the hydropower canal on the river network and subsequently by sample size, the model's predictive success in the Otamatapaio riverscape indicates transferability through space as well. The Otamatapaio modelling result is especially encouraging, as *G. vulgaris* had a much narrower distribution than in the training dataset, indicating model robustness to different configurations of source and sink habitat. While the role of source location has previously been demonstrated to drive sink-habitat occupancy (Nol et al. 2005),

my model also indicates spatial habitat configuration can have a predictable effect on the outcome of interspecific interactions.

These results suggest that with sufficient initial understanding of the interaction between species and their habitats, digitised habitat data could be used to predict outcomes of interspecific interactions or other biotic processes. This may be especially true in rivers, where the role of habitat configuration in driving population, community and ecosystem dynamics has become increasingly clear (Fausch et al. 2002, Malmqvist 2002, Thorp et al. 2006).

The predictive ability of such models will depend on availability and quality of animal distribution and geographic data. Validation of my electrofishing technique indicated a few *G. vulgaris* occurrences in the exclusion zone might have been missed (the species had a probability of detection of 0.72). These false absences were associated with low density, potentially transient occupation of exclusion reaches, rather than local populations capable of persisting over time. The predictive capacity of the model and the ecological significance of the distribution patterns would thus be robust to such modelling errors.

Regarding geographic data requirements, my study needed a spatial model of New Zealand rivers that could represent fish habitat at the appropriate scale, representing both network configuration and stream size with sufficient accuracy. As such, critical local-scale features such as small spring-fed tributaries were not always represented in the FWENZ. Consequently, one of the source streams in the Otamatapaio riverscape is not present in the FWENZ model, and I instead placed the associated trout barrier on the nearest stream at the location of their confluence. This example indicates the necessity of ground-truthing network configuration of demographic sources and altering existing geographic data to reflect reality where appropriate.

Another potential drawback to the simplicity of the current exclusion model is that it lacks reference to the effect of flood disturbance on trout-galaxiid interactions. High-velocity flooding events negatively affect trout distributions in New Zealand (Jowett and Richardson 1989, Jowett 1990). Such disturbance, assessed by comparing the stability of riverbeds among study sites, appears to enable co-occurrence of *G.*

vulgaris and trout far from sources (Chapter 4). Existing representations of riverbed disturbance, such as the gravel layer in the New Zealand Landcover Database (Ministry for the Environment 2002), were investigated but were not sufficiently accurate to fulfil this purpose during model development. Higher resolution remote sensing technologies could substantially improve detection and modelling of river disturbance (Lane et al. 2003, Marcus and Fonstad 2008), and should be investigated for future derivations of the model.

When habitat measurements are used to predict the outcome of interspecific interactions, ecological information other than geographic data will also be needed. In the galaxiid exclusion model, a critical criterion for successfully running the model was knowledge of all *G. vulgaris* source populations. Incorrect diagnosis of source locations affected the Fraser riverscape, where the initial assumption of one demographic source resulted in a clearly inaccurate initial model. In this case, the riverscape upstream of the Pukaki hydroelectric canal appeared to act as a demographic source for *G. vulgaris*, despite trout being present in some reaches upstream. Once upstream reaches were re-designated as sources, however, the low number of remaining sites hampered statistical validation of the model. This validation failure illustrates the need for sufficient sampling in both the modelled inclusion and exclusion zones to validate the model.

Since fish surveys are needed for model validation, as well as to correctly identify source populations for *G. vulgaris*, the galaxiid exclusion model is likely to be most effective when applied in an iterative fashion. To work as a viable desktop tool for managers, trout-invaded riverscapes with known barrier populations of *G. vulgaris* should be used, the model applied and the results compared to existing patterns of galaxiid-trout co-occurrence. When multiple unexpected presences occur in the exclusion zone, surveys can be directed to specific reaches of the riverscape to seek potential unknown source populations and to add survey records to improve the validation dataset. The model could then be re-run with improved model assumptions and validation data.

A conservation spin-off of this process would be identifying areas in which to search for undiscovered *G. vulgaris* source populations. I assessed this utility by using the

model to define a search radius for potential unknown demographic sources of *G. vulgaris* in the Otamatapaio River, and identified four potential trout-free streams based on the analysis. While initial pilot surveys suggested these tributaries to be fishless, further, more intensive fieldwork would be required to establish whether *G. vulgaris* were present or whether the unexpected occurrence was an artefact of the model's current simplicity.

By identifying critical barrier populations, the model could help in managing invader populations. The exclusion of aquatic invasive species is a critical function that terrestrial reserves do not generally perform (Saunders et al. 2002). The designation of source streams above trout barriers as conservation "focal areas" (*sensu* Abell et al. 2007), independent of existing conservation structures, could enable targeted conservation management. By protecting the source stream without needing to purchase the surrounding land, conservation authorities would have greater wherewithal to enforce protection of instream habitats and prevent future invasions across multiple river networks. This solution could enhance overall security of *G. vulgaris* and other non-diadromous galaxiids threatened by trout.

Models of the kind described here could also be used to increase the efficiency of active galaxiid population management. Since trout have an overriding effect on galaxiid persistence compared to habitat quality (Townsend and Crowl 1991, Chapter 2), traditional management efforts such as habitat restoration may not improve galaxiid population viability in trout-invaded streams. A more beneficial strategy would be to remove trout from streams where they exert the highest predation pressure. Trout eradication operations have been conducted with piscicides to the benefit of galaxiids in Australian streams (Lintermans 2000). Because the size and length of streams targeted will affect logistic feasibility of trout-removal operations (Moore et al. 1986), stream selection will likely depend on cost-benefit analyses. By running different scenarios of the model where demographic source streams are added or expanded in the riverscape, operations that maximise expansion of the co-occurrence zone with minimal recovery of trout-free habitat can be preferentially selected. Thus the model can aid managers in increasing *G. vulgaris* population viability across trout-invaded riverscapes.

Models that use habitat to predict interspecific interactions have great potential as conservation management tools, due to the simplicity of input data used to generate ecological data that are useful to managers. It remains to be seen whether other examples of biotic interactions involving threatened species exist that could be modelled in this fashion. In order to obtain the prerequisite knowledge to design such models, effort must be made in ongoing field studies to assess whether habitat has a consistent effect on biotic interactions across a landscape. Once such an effect is recognised, researches will need to assess the spatial context of biotic interactions, determine at which scale the interaction is best modelled at, and seek appropriate digital habitat data on which to base the model. Only through seeking out these patterns, will the full potential of this modelling approach be revealed.

ACKNOWLEDGMENTS

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Plate 5: The Broken River, Waimakariri Basin: a hostile riverscape for non-diadromous galaxiids.

Chapter 6

Conserving non-diadromous galaxiids across trout-invaded riverscapes

Introduced trout are recognised as a significant threat to the conservation of galaxiid fishes in New Zealand and across the southern hemisphere (McDowall 2006). The threat posed by trout to non-diadromous galaxiids is dependent on the strength of interactions and these are likely to vary with habitat conditions across invaded networks (McIntosh 2000). In this thesis I investigated whether trout created demographic sinks in two species of non-diadromous galaxiids, the Canterbury galaxias (*Galaxias vulgaris* Stokell) and the alpine galaxias (*Galaxias paucispondylus* Stokell). By assessing patterns of juvenile recruitment, I established that trout did create sinks in *G. vulgaris* populations. In contrast, trout did not appear to create demographic sinks in *G. paucispondylus* populations. This species' thin body shape may allow it to better utilise interstitial cover in the riverbed and macrophyte beds to avoid trout predation, compared to the more robust *G. vulgaris*. Having found evidence of source-sink dynamics in *G. vulgaris*, I assessed how variability of instream habitat and spatial configuration of trout-free refuge populations affected the species' occurrence in trout-invaded streams. A spatially explicit pattern of exclusion of *G. vulgaris* by trout was detected within sink reaches, and I developed a GIS-based model to predict this exclusion pattern in other systems where *G. vulgaris* and trout co-occur. This chapter summarises the major findings of the previous chapters and discusses their implications for conserving non-diadromous galaxiids and other threatened fish species that reside in invasive predator-dominated riverscapes. The chapter will be used as the basis for a New Zealand Department of Conservation "Science for Conservation" publication, and has been structured with this eventual output in mind.

The riverscape-scale impact of trout on non-diadromous galaxiid populations

Trout have been long been assumed to pose both a predatory and competitive threat to non-diadromous galaxiids, due to their dietary overlap and complementary distributions with many species (Townsend 1996, McDowall 2003a). Previous

experimental studies, conducted in artificial channels and mesocosms, have shown galaxiids of the *'G. vulgaris sensu lato'* group (i.e. "roundhead" and "flathead" galaxiids) to be vulnerable to competitive displacement by small (<150 mm FL) trout and direct predation by large (>150 mm FL) trout (Glova et al. 1992, Glova and Sagar 1993, McIntosh et al. 1994, McIntosh 2000). In this study, a fish manipulation experiment in a natural stream and two mesocosm experiments indicated brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum) both pose a significant predatory threat to *G. vulgaris* and *G. paucispondylus* (Chapter 3). The implication of this finding is that wherever either brown or rainbow trout occur in sufficient numbers in a river network, the threat of predation on non-diadromous galaxiids will be high.

A series of spatially extensive, low intensity electrofishing surveys were conducted across the upper reaches of the Broken River and its major tributary, the Porter River, in the Waimakariri River catchment during summer 2007 and autumn 2008. Trout occupied the majority of surveyed habitat in all tributaries of both rivers (Table 1). Because the research took place in the headwaters of these rivers, the proportion of trout-free habitat is actually higher than it would be across the entire catchment. It is estimated that trout occupy >95% of all fish-occupied habitat in the Waimakariri River catchment, based on current fish distribution records (McIntosh et al. 2010). While *G. vulgaris* was recorded in many trout-invaded reaches, recruitment of post-larval galaxiid fry was limited to 9% of trout-invaded reaches in the Broken River (Chapter 2). The majority of trout-invaded habitat was a demographic sink for *G. vulgaris*, and the lack of juvenile recruits captured by depletion electrofishing indicated that population persistence was driven primarily by immigration of adults from trout-free reaches (Chapters 2 and 4). Trout-free sites, with their high juvenile recruitment, appeared to act as sources of immigrants for the trout-invaded sink reaches (Chapter 2, Figure 1).

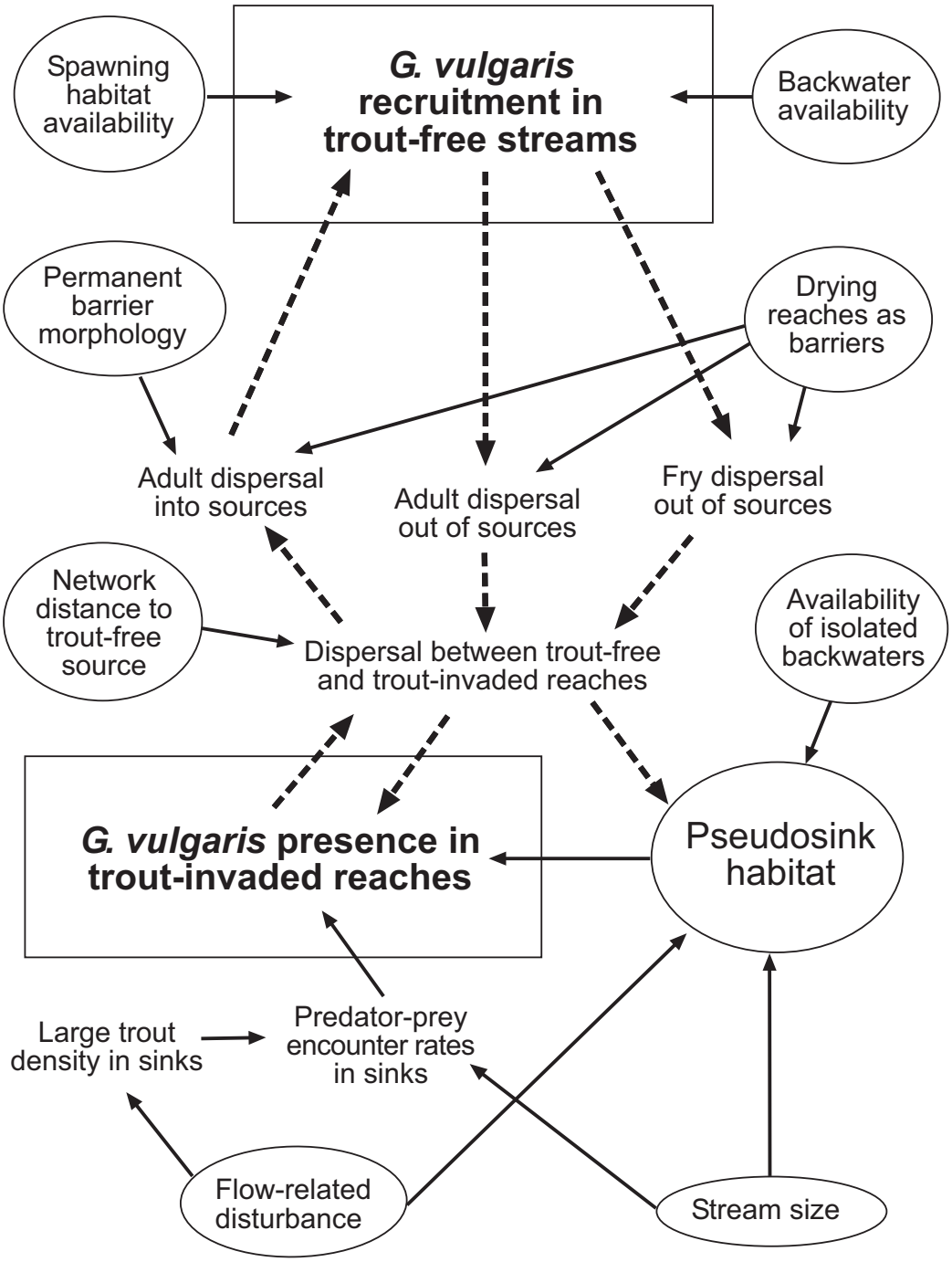

Figure 1: Processes that drive *G. vulgaris* occurrence patterns in trout-invaded riverscapes. Solid arrows depict mechanisms affecting *G. vulgaris* dispersal and persistence, while dashed arrows represent dispersal pathways between trout-free and trout-invaded habitats. Circles represent habitat drivers of these ecological processes.

Table 1: Comparison of length of fish-occupied habitat upstream and downstream of trout barriers in the upper Broken and Porter rivers.

	Total length of stream (km)	Percentage stream length
Trout-free	5.1	14%
Trout invaded	30.1	85%

The Broken and Porter Rivers both support well established trout populations, so that the effect on *G. vulgaris* was predictably severe. The consistency of trout impacts across other catchments will depend on the density and distributions of large trout. Habitats disturbed by seasonal flooding and drying have depleted trout biomass (McIntosh 2000, Chapter 2), and in this study large predatory trout were seasonally restricted to hydrologically stable reaches (Chapter 4). Because trout densities are impacted by individual disturbance events (Jowett and Richardson 1989), trout effects on galaxiids in streams with severe disturbance regimes are likely to fluctuate over time. In the Cass River, a highly disturbed tributary of the Waimakariri River, annually monitored trout densities decreased with recent (last three months) rainfall, demonstrating the temporal role of flood disturbance in driving habitat occupancy by trout (McIntosh et al. 2010). Sustained hydrologic disturbance appears important in allowing co-existence of trout and non-diadromous galaxiids in streams (Closs and Lake 1996, Leprieur et al. 2006). Consequently river networks that offer consistently marginal habitat for trout will decrease the likelihood of demographic sinks forming, as was the case in a small proportion of the Broken and Porter rivers.

Even in systems like the Broken River where the majority of the river network is suitable for sustained trout occupancy, local reach-scale factors will mediate the impact of trout on local galaxiid population persistence. Predation is determined largely by encounter rates, which in turn can be mediated by predator and prey densities, as well as habitat complexity (Crowder and Cooper 1982, Morin 1986, Beukers and Jones 1998, Seitz et al. 2001). Habitats that support high predator densities will be hostile habitats for prey species, unless local habitat heterogeneity can disrupt predator feeding efficiency or provide refugia that are inaccessible to the predator (Crowder and Cooper 1982, Steele 1999, Kauffman et al. 2007). As use of

habitat by fish shifts ontogenetically with time, different types of stream habitat are likely to provide critical refugia for different life-history stages (Schlosser 1987, Schlosser 1988).

At the post-larval or "fry" stage, *G. vulgaris* is confined to backwaters with low flow, a stage when they are extremely vulnerable to predation by trout of all sizes (McIntosh et al. 2010, Chapter 2). In a riverscape context, backwaters may act as refugia for *G. vulgaris* fry if they are temporarily disconnected from the main channel, or if trout densities in the adjacent stream are low enough that the backwater is not exploited during the course of the summer. In the Broken River, the majority of trout-invaded reaches (91%) contained no fry at the end of summer, rendering these reaches demographic sinks for *G. vulgaris* (Chapter 2). The few reaches where sporadic *G. vulgaris* recruitment occurred were considered "pseudosink" habitat (after Pulliam 1996), as they appeared to support low densities of both trout and galaxiids. These reaches could support limited persistence of *G. vulgaris* within trout-occupied networks, but would be highly susceptible to extinction in comparison to trout-free source populations (Chapter 2). Pseudosink sites are likely to have a low carrying capacity for galaxiids and trout through their lack of invertebrate food resources due to the high rate of habitat disturbance by flooding (Death and Winterbourn 1994, Suren and Jowett 2006). Increased displacement and mortality of individual fish, as well as disruption of spawning by frequent flooding or drying (Allibone 2000, Detenbeck et al. 1992), would also directly affect the persistence of both galaxiid and trout populations in these reaches.

In contrast to *G. vulgaris*, *G. paucispondylus* recruitment does not appear as heavily affected by the presence of trout. The fry may be far more agile and benthic in behaviour, and may be more resistant to predation from trout entering a backwater (Chapter 3). The ability of trout to create demographic sinks for *G. paucispondylus* requires further investigation. *Galaxias paucispondylus* appeared to achieve maximum juvenile recruitment in disturbed sites with minimal trout occupancy. In contrast to *G. vulgaris*, however, G. paucispondylus juveniles co-occurred with trout in streams of varying size and disturbance, provided summer water temperatures were below an apparent physiological limit of 18ºC. It appears *G. paucispondylus*' elongated form allows them to use interstitial and vegetative cover in the riverbed

more effectively than *G. vulgaris*, potentially minimising encounter rates with trout. However, much remains to be learned about the direct and indirect effects of trout on *G. paucispondylus* population health over time (Chapter 3).

Adults of both *G. vulgaris* and related flathead species appear to partially avoid trout by occupying different microhabitats in a stream reach (McIntosh et al. 1992, Glova and Sagar 1993). Increased area and morphological heterogeneity in a stream reach could potentially decrease encounter rates between predators and prey (Angermeier and Schlosser 1989). Thus larger, more morphologically complex streams should enable more prolonged persistence of *G. vulgaris* in trout-occupied sink habitats. Persistence in these habitats will however also depend on immigration from demographic sources in trout-free tributaries, together with the availability of predation refugia for adult galaxiids. Thus a mosaic of interacting physical, biotic and spatial drivers will ultimately dictate *G. vulgaris* persistence (Figure 1).

A remarkable feature of the *G. vulgaris* metapopulations studied were that trout-free reaches occupied such a small percentage of the fish occupied habitat (Table 1), yet still appeared to act as viable demographic sources in the riverscape. Especially notable was the generally small size of trout-free habitats (Table 2), which nonetheless supported large galaxiid populations with relatively healthy demographic characteristics (Chapter 2). A major management implication of this research is that for trout-free streams to function as demographic sources for galaxiids in a trout-invaded riverscape, their number and location within the river network may be far more important than their dimensions or longitudinal extent. Of potential concern to managers is that these refuge streams are not easy to diagnose without fieldwork, as they are often indistinguishable from fishless streams on a map. The barriers that protect them from trout are also physically variable and could easily be overlooked. Trout barriers in the Waimakariri catchment were not always physically substantial, and trout breached some during the course of this study. For example the upper reaches of Coach Stream, a tributary of the Kowai River, were apparently inaccessible to trout due to a road culvert until 2007, when trout were discovered upstream. This incident highlights the need to continuously monitor existing barriers and seek out new ones to maximise population security of non-diadromous galaxiids.

Table 2: Length and dimensions of trout-free streams above trout barriers that appear to have functioned as demographic sources for *G. vulgaris*.

Stream	Barrier type	Fish-occupied length (m)	Mean width (m)	Mean depth (cm)
Skifield Stream *	road culvert	168	1.5	20
Dry Stream	drying reach + road culvert	788	2.9	24
Bradley Stream *	drying reach	1051	1.1	25
Thunder Creek * †	bedrock chute	1476	1.6	31
Parapet Stream * †	waterfall	1089	1.8	30
Otamatapaio River (terrace tributary) †	waterfall	50	1.3	22
Otamatapaio River (headwater tributary) †	waterfall	unknown	1.8	46
Fraser River (unnamed spring creek) †	road culvert	unknown	0.7	30

* Unofficial name

† Dimension data represents electrofished reaches only, not all fish-occupied habitat

Effects of source configuration and connectivity on *G. vulgaris* distributions

Spatially-explicit analysis of the relationship between *G. vulgaris* occurrence and various habitat features in the Porter and Broken riverscapes revealed a pattern of spatial exclusion, where *G. vulgaris* was consistently absent from small, stable streams far from the nearest trout-free tributary in the network (Chapter 4). The combination of narrow stable habitats occupied by large trout, with minimal immigration of adult galaxiids dispersing from sources, appeared to drive this spatial pattern.

There was a potential interaction between stream size and disturbance in defining the exclusion zone in the Broken and Porter Rivers, as many large sink reaches where *G.*

vulgaris occurred also had high flood-related bed disturbance (Chapter 4). The relative importance of disturbance and stream size in prolonging *G. vulgaris* occupancy of trout-induced sink streams requires further investigation in streams where large stable and small disturbed reaches occur far from source streams. Nonetheless, the implication of the pattern is that the nearer a sink reach is to a source, the more immigrating adults are likely to sustain occupancy of the sink reach over time.

To confirm and quantify the underlying mechanism of dispersal from sources to sinks, further research will be needed to estimate dispersal rates both across trout barriers and through sink reaches. Mark-recapture and PIT tagging studies can offer valuable insights into freshwater fish dispersal patterns, although they offer unique logistical challenges to implement (Labbe and Fausch 2000, Homel and Budy 2008). Mark-recapture has been used in a limited capacity on *G. vulgaris*, and has demonstrated mobility to be strongly linked to spawning behaviour (Cadwallader 1976a). The use of molecular markers such as microsatellites (e.g. Hänfling and Weetman 2006) could also offer crucial information on dispersal rates between sources and across sink reaches.

It is likely the spatially explicit patterns of *G. vulgaris* exclusion would not have been detected without an extensive, low intensity spot-fishing sampling regime (Chapter 4). Standard fish diversity and distribution monitoring protocols, such as the American EPA wadeable stream guidelines, call for a limited number of long (e.g., 40 times the stream width) sampling reaches to capture maximum fish diversity in a river (Peck et al. 2001). This method could potentially misrepresent the presence or prevalence of *G. vulgaris* within a trout-invaded river if a single representative site was placed far from the nearest source. My technique, while far less intensive than the EPA approach, detected effects of spatial habitat configuration on a target species through the high number and dispersion of sample sites across the river network. Conservation managers, when planning survey regimes for threatened fish, should consider the trade-off between efficiently detecting local fish assemblage characteristics (which may be affected by landscape-scale rather than local-scale drivers) and assessing landscape-scale distribution patterns of individual species.

Source-sink metapopulations maintain stability through the rescue of sink patches from extinction via dispersal from source patches (Dias 1996). Increasing the number of source populations in a river network may not only increase overall metapopulation stability, but could also affect population persistence in trout-invaded reaches through increased supply of dispersing fish. Because dispersal through sink habitat can decrease extinction risk in both source and sink populations (Foppen et al. 2000), the viability of *G. vulgaris* populations in both trout-invaded and trout-free habitats could depend on dispersal to and from sources, and across sink reaches (Figure 1). Maintaining connectivity to allow dispersal between sources and sinks is a thus fundamental driver of metapopulation stability (Namba et al. 1999, Fagan 2002, Hilderbrand 2003). A primary driver of such connectivity in *G. vulgaris* source-sink metapopulations is the morphology of trout barriers (Figures 1 and 2).

Figure 2: Three examples of trout barriers, each displaying a different permeability for dispersing galaxiids. Shown from left to right are a seasonally drying reach (Dry Stream, Porter River catchment), a bedrock chute passable by climbing galaxiids but not leaping trout (Thunder Creek, Broken River catchment), and an overhanging waterfall that is unlikely to be scalable by trout or non-migratory galaxiids (Parapet Stream, Broken River catchment). Further details of these streams are listed in Table 2.

Dispersal from sources to sinks by *G. vulgaris* fry is likely to be common across waterfall and culvert barriers, as passive drift is their primary mode of dispersal (Cadwallader 1976a, Jellyman and McIntosh 2008). Adults in comparison may be less

likely to actively disperse over waterfalls, and will not be able to re-enter the source if the morphology of the waterfall prevents it (Figures 1 and 2). Barriers such as bedrock chutes (Figure 2), may be scalable by galaxiids such as *G. vulgaris* and *G. depresseceps*, which can climb them by crawling (Allibone and Townsend 1997, McDowall 2003b). In contrast, such barriers are not passable by trout as they require leaping from a deep pool below a barrier to scale it (Bjornn and Reiser 1991). These barriers may allow more exchange between source and sink populations of galaxiids than waterfalls, while being equally impervious to trout invasion.

Seasonally drying barriers are highly conducive to active dispersal by adult *G. vulgaris*, which tend to rapidly colonise re-wetted reaches of intermittent streams (Davey and Kelly 2007). However, the timing of stream drying is likely to be critical both for preventing trout invasion and for allowing dispersal into sinks. For example, wetted periods during trout spawning, when adults migrate upstream in search of redds (Ovidio et al. 1998), may precipitate penetration upstream of the barrier. Conversely, disconnected flows during months of peak fry dispersal could greatly inhibit dispersal of fry to downstream reaches. Moreover, the benefits of habitat drying for minimising trout-galaxiid interactions are likely to be delicately balanced with the negative impacts on galaxiid populations, such as loss of critical spawning habitat and direct mortality (Allibone 2000, Leprieur et al. 2006), and require more detailed study.

Small, stable trout-invaded streams, by virtue of their low habitat heterogeneity and high resident trout biomass, are likely to inflict the highest predation pressure on *G. vulgaris* and are the most in need of immigration from sources to support their long term occupancy by galaxiids (Chapter 4). Conversely, they are also the most logistically feasible streams for trout eradication operations, due to the increase in resources and time required to treat larger streams (Moore et al. 1986). Management plans for conserving galaxiids should assess the costs and benefits of active rehabilitation projects (Peterson et al. 2008). For example, creating a new barrier on a tributary, removing trout upstream and introducing galaxiids could be a feasible way to add a demographic source. The position of the barrier and consequent upstream length to be treated, the structure and permeability of the barrier to galaxiids, as well

as its location relative to other sources in the network will all need to be considered when assessing the feasibility of such operations.

Modelling the ability of trout to exclude *G. vulgaris* and its relatives

To determine whether *G. vulgaris* co-occurrence with trout could by predicted in streams outside the Waimakariri catchment, I developed a GIS-based model that used landscape-scale habitat data and network distances to predict where trout would exclude galaxiids in a sink network (Figure 3). The model correctly predicted *Galaxias vulgaris* distributions in the Otamatapaio River in the Waitaki River catchment (Chapter 5), indicating the exclusion phenomenon was unlikely to be an artefact of distributions in the training catchments.

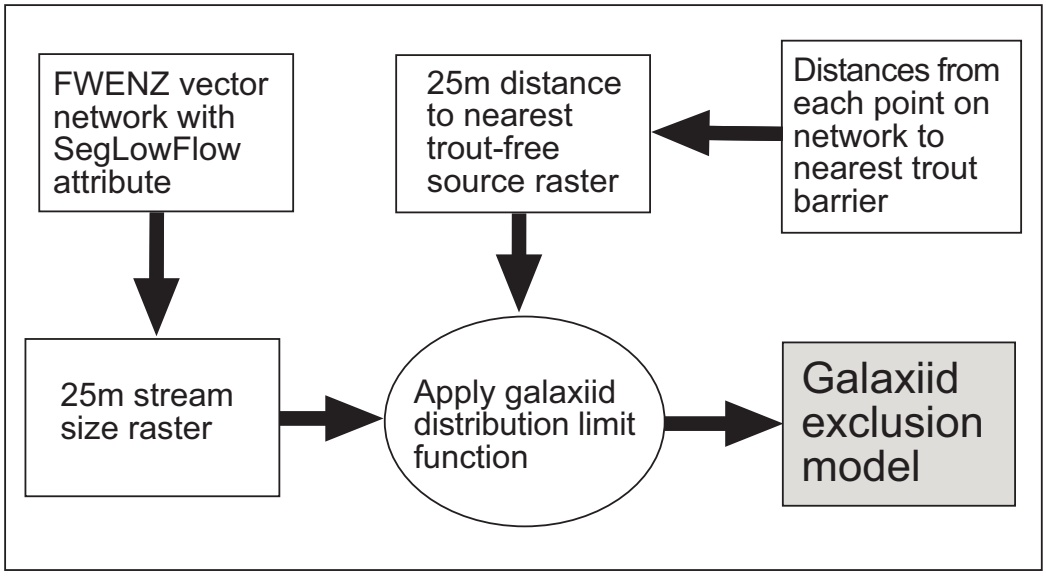

Figure 3: Modelling procedure used to derive the galaxiid exclusion zone in a stream, based on stream size and distance to the nearest trout barrier. The SegLowFlow attribute of the FWENZ model of New Zealand river networks is an estimate of mean annual low flow that is used as a surrogate for stream size. The galaxiid distribution limit function is a linear equation that uses the distance and size rasters to calculate the maximum distance *G. vulgaris* should occur from trout barriers. The exclusion model determines which reaches in the river network model fall outside the modelled limit of *G. vulgaris* occurrence relative to the barriers. All procedures were performed in ArcGIS 9.1 using the Model Builder application.

Critical criteria for using the model included knowledge of trout occupancy in the invaded riverscape, the location of all galaxiid demographic sources, and having sufficient fish occurrence data both inside and outside the modelled exclusion zone to run the model (Chapter 5). The model can operate as a versatile management tool for galaxiid conservation, if used in an iterative fashion, based on a sequence of decision-based procedures (Figure 4). Once existing localities of both trout barriers and *G. vulgaris* occurrences are placed on a river network and their distances digitised, exclusion zones based on the interaction between distance-to-source and stream size can be predicted. If many occurrences are located within the modelled exclusion zone, this could be a sign of unknown source populations within the modelled network. Physical factors such as disturbance that limit trout distributions could also result in inaccurately modelled exclusion zones, and the physical attributes of a river and the consistency of trout occupancy in the invaded network should be carefully considered when applying the model (Chapter 5, Figure 4).

Provided it is used appropriately, the model will be a useful tool for detecting unknown source populations using unexpected galaxiid presences in the exclusion zone. The priority for managers once a barrier is found should be to determine the nature and security of a barrier and ensure that the landowners or relevant authorities (if on Department of Conservation or Crown land) are aware of the need to keep the stream trout-free. Because current conservation structures (national parks, conservation areas) exist at a scale inappropriate for protecting newly discovered source populations, new methods of protecting these critical habitats will be needed. One such approach would be to declare these streams freshwater protected areas independent of the established conservation estate (following Abell et al. 2007), thus conserving the entire metapopulation regardless of whether the river network it occupies flows through public or private land.

Another practical use of the model would be to visualise active management of scenarios such as expanding an existing source population by moving the trout barrier downstream, or by eradicating trout from a tributary and translocating galaxiids to create a new trout-free source population. Both refuge habitat expansion (Lintermans 2000) and translocation (Harig and Fausch 2002) would have positive effects for native fish populations threatened by invasive salmonids, if managed correctly.

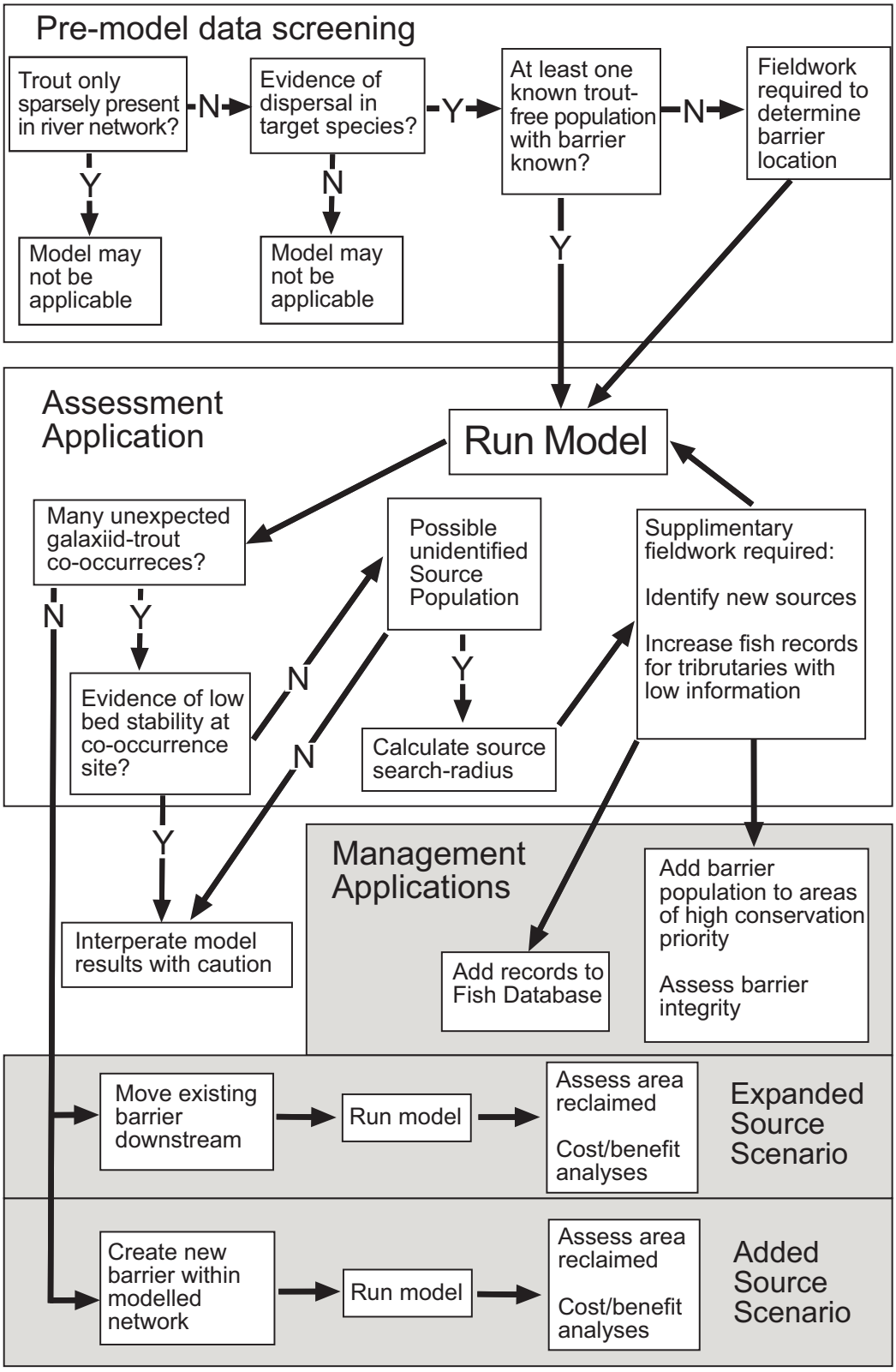

Figure 4: Procedures for using the galaxiid exclusion model as a management tool to conserve galaxiids in trout-occupied riverscapes. Steps with direct management application are boxed in grey.

By modelling the outcomes of different intervention strategies, projects that maximise the potential for expanded co-occurrence and population persistence in trout-invaded sinks could be preferentially selected.

As an example, Figure 5 illustrates two scenarios where trout eradication and galaxiid translocation were performed in the headwaters of the Porter River, upstream of the Porters skifield. In the first scenario, 1.5 km of stream is cleared and a barrier placed on the headwater tributary draining Coleridge Pass. The model predicts that this new source would support co-occurrence of galaxiids and trout for 730 m downstream (Figure 5a). A second scenario uses the same effort to clear an identical length of trout invaded habitat in a downstream tributary. Due to the larger size of the Porter River downstream of the confluence with this stream, the model predicts co-occurrence could be enabled over as much as 1.85 km (Figure 5b). The model predicts that source streams that flow into large rivers are likely to have a bigger effect on overall co-occurrence as increased area, habitat heterogeneity and the potential for high energy flood events would lower predation pressure by trout compared to smaller headwaters (Chapter 4). Thus, a short, narrow tributary that flows into a large, physically heterogeneous river would be an ideal candidate for a rehabilitation project.

For the galaxiid exclusion model to be of maximum utility to galaxiid conservation in New Zealand, it would be useful if it provided insight into the management other non-diadromous galaxiids considered to be threatened and in need of active conservation management (Department of Conservation 2004). My research has shown that there are fundamental differences between *G. vulgaris* and *G. paucispondylus* in their spatial interactions with trout (Chapter 3), and it is likely that other pencil galaxiids such as *G. prognathus*, *G. cobitinis*, *G. macronasus*, and *G. divergens* will interact with trout in ways more closely resembling *G. paucispondylus*. Further research into the spatial interactions between trout and these species could enable new management tools like the galaxiid exclusion model to be developed for pencil galaxiids.

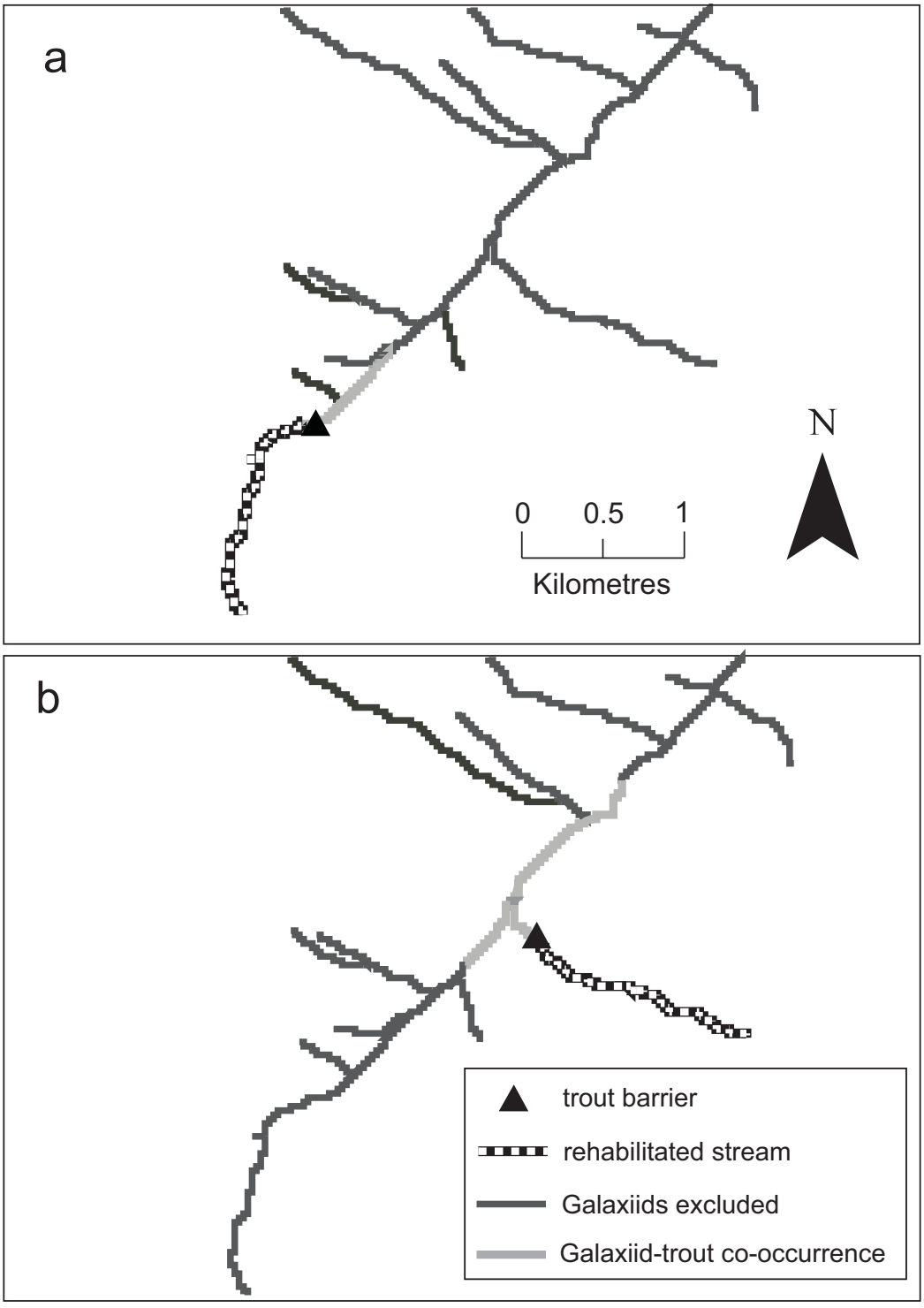

Figure 5: Maps of modelling scenarios generated by the galaxiid exclusion model showing lengths of potential galaxiid-trout co-occurrence habitat created by a) removing trout and restoring galaxiids to the headwaters of the Porter River and b) restoring the identical amount of habitat on a downstream tributary

It was notable during fieldwork in the Otamatapaio and Fraser Rivers in the Waitaki catchment that *G. cobitinis* and *G. macronasus* were seldom found in the same stream as trout and never in the same microhabitat. It is likely that these species are restricted both by habitat requirements and trout (McDowall and Allibone 2004, Elkington and Charteris 2005). It is therefore likely that critical interactions between trout and these galaxiids take place at a smaller spatial scale than the *G. vulgaris* model operates at.

For the galaxiid exclusion model to be applied to galaxiids of the roundhead and flathead morphological groups, two fundamental assumptions need to be considered. First it is assumed that trout occupy the majority of the trout-invaded riverscape, and secondly it is assumed that some dispersal from trout-free streams into trout-occupied streams occurs (Figure 4). Genetic differentiation between populations of *G. depressiceps* separated by waterfalls implies there is little dispersal across these barriers (King and Wallis 1998), though it is unclear if this pattern was the result of the morphology of the barriers in the study or indicative of a broader trend in the species. Similarly, populations of the roundhead *G. gollumoides* and the undescribed "southern flathead galaxias", occurring in trout-free streams in Southland, both showed sufficient intraspecific genetic variability to suggest limited gene flow between these populations (Crow et al. 2009). It remains to be established what level of isolation causes the genetic structuring of non-migratory galaxiids observed at the reach scale, so the possibility of regular cross-catchment dispersal in flathead and roundhead galaxiids cannot be ruled out.

Assuming that dispersal does link trout-free and trout-invaded populations, the galaxiid exclusion model could provide a useful tool for assessing the spatial interactions of trout and galaxiids and highlighting knowledge gaps that could impede galaxiid conservation. For example, preliminary modelling of exclusion zones for *Galaxias depressiceps* in the Taieri River catchment and the undescribed "Clutha flathead galaxias" in the Clutha River catchment produced mixed results, with many galaxiid occurrences (taken from the New Zealand Freshwater Fish Database - NZFFDB) located within the modelled exclusion zone. This may be an indicator of multiple unknown barrier populations, as there are only three confirmed barrier locations for *G. depressiceps* in the records of the DoC Otago Regional Office (Simon Madill, Department of Conservation, pers. comm.). However, the sparse NZFFDB

records of trout in many of the modelled tributaries also suggest that patchy trout distributions rather than unknown sources could be the reason for many unexpected galaxiid occurrences in the model. Regardless of the reasons for unexpected results, the model could aid managers by pointing to these gaps in our current understanding of galaxiid-trout co-occurrence, and highlighting critical areas for future fieldwork. Through iterative use of the model and targeted fieldwork as outlined in Figure 4, it could provide a starting point for developing more detailed research and management strategies for non-migratory galaxiids in trout-invaded riverscapes.

Conclusions

My research has illustrated the complex role landscape habitat configuration can play in mediating the effects of introduced predators on native prey. The spatially explicit nature of the interaction highlights the importance of explicitly examining dispersal pathways when assessing population structuring across landscapes. The role of habitat patch size and isolation in driving metapopulation stability has long been acknowledged (Namba et al. 1999, Ficetola and De Bernardi 2004, O'Brien et al. 2008). My study has provided insight into how the spatial configuration of patches and the pathways between them can affect the dynamics and distribution of species affected by an invader, especially in the confined structure of a dendritic network. While configuration of high and low productivity habitat in networks have been linked to source-sink dynamics in fish populations before (Pringle 2001, Fagan 2002, Schick and Lindley 2007), my research indicates such mechanisms are just as important for prey populations in networks dominated by invasive predators.

Identifying and protecting dispersal routes between sink and source populations is crucial for restoring threatened fish populations (Schick and Lindley 2007). The dispersal-distance mediated exclusion of galaxiids by trout suggests preserving connectivity between predator-free sources and predator-dominated sinks may even be more important for overall metapopulation stability than improving habitat conditions in individual habitat patches. Nevertheless, the minimum critical size and habitat requirements of source populations for most non-diadromous galaxiids remain unknown (Department of Conservation 2004). Further research into potential drivers of recruitment success in the absence of predators, such as adult spawning and fry

recruitment habitat, is crucial for both extant and potential source streams to be correctly managed.

Galaxias vulgaris metapopulations in trout-invaded networks represent a challenge to conservation managers, in that conservation efforts like habitat restoration are far less likely to have positive outcomes if the spread of invaders is not also kept in check. Managers of native fish threatened by invasive fish often face a dilemma as to how to prevent invasion without also disrupting connectivity between trout-free sources and trout invaded sinks (Fausch et al. 2009). For example, the conservation of endangered salmonids in the United States, which are threatened by both invasive salmonids and habitat fragmentation (Dunham and Rieman 1999, Harig and Fausch 2002), relies on managers being able to carefully weigh the cost and benefits of particular management actions. By isolating individual populations in order to protect them from predation, competition and hybridisation with invasive salmonids, they may inadvertently increase their stochastic extinction risk (Harig and Fausch 2002, Peterson et al. 2008, Fausch et al. 2009). In the case of galaxiids and trout, their differing morphology and locomotion means it may be possible to design barriers that prevent passage by salmonids while allowing passage by galaxiids. This problem will differ for each species facing the threat of invaders, and will need to be examined case by case to find appropriate solutions.

To ensure the survival of non-diadromous galaxiids and other fish species threatened by invasive predators, the extent of invader-free source populations must be maintained, and the creation of new demographic sources actively pursued. To achieve the former task, source populations need legislative protection in order to guard against habitat degradation and deliberate introduction of introduced predators. While terrestrial conservation areas seldom protect river networks from introduced species (Pringle 2001, Saunders et al. 2002), such protection could be achieved by designating invader-free streams freshwater protected areas (FPAs). The recognition of core habitats for maintaining metapopulations is a key advantage of FPAs over terrestrial conservation areas (Saunders et al. 2002). In the case of invader free-source populations, the designation of the streams they inhabit as freshwater conservation "focal areas" (following Abell et al. 2007) would allow conservation authorities to enforce protection of these spatially restricted habitats without needing to buy large

tracts of surrounding land from the landowner – a crucial drawback of terrestrial reserves. Moreover, protection of these areas need not unnecessarily restrict the use of surrounding land, as long as critical management practices such as prohibition of predator introductions and preservation of riparian habitats are enforced (Abell et al. 2007).

The task of creating new invader-free source populations is the ultimate practical method to reinforce these threatened metapopulations. Projects to remove invasive predators from streams can present prohibitive logistical challenges (Moore et al. 1986, Shepard et al. 2002), and risk failure should these habitats be unsuitable for native fish recruitment (Harig and Fausch 2002). Consequently management tools like the galaxiid exclusion model must continue to be developed and improved to maximise the chances of successful interventions. Ultimately, only through active management and co-ordinated practical responses to new threats (such new predator invasions), will we assure the conservation of native species in invasive predator-dominated riverscapes.

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